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WITH NINETEEN PLATES AND ONE HUNDRED AND THIRTY-ONE FIGURES

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## ERRATA.

VOLUME XXXVII—

    P. 450, line 19, for cones read ones.

    P. 450, line 3 from below, for as read or.

    P. 451, line 5, for fallen read galled.

    P. 452, line 7 from below, for found read formed.

    P. 454, line 17, for abuses read absence.

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    P. 80, line 9 from below, for Pathology read Physiology.

    P. 83, line 4 from below, for he read the.

    P. 89, line 8, for precesses read processes.

    P. 89, line 8, for oogonesis read oogenesis.

    P. 92, line 5, for oogonesis read oogenesis.

    P. 160, line 2, for societv read society.

    P. 163, line 10 from below, insert as after pericycle.

    P. 298, line 11 from below, for Coixdactyloides read Coix dactyloides.

    P. 391, line 0 from below, for mycological read cytological.

# BOTANICAL GAZETTE

## *JULY, 1904*

### SPERMATOGENESIS AND OOGENESIS IN EPHEDRA TRIFURCA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LIX.

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(WITH PLATES I–V)

THE Gnetales are exceedingly important from a morphological standpoint because of many points of contact with angiosperms. That they have not received the attention their character warrants is probably due to the difficulty encountered in obtaining material suitable for critical morphological study.

Ephedra, comprising about twenty species, is confined to the warmer arid regions of the northern hemisphere, and is evidently more nearly related to the Coniferales than is either Tumboa or Gnetum.

Important morphological literature dealing with Ephedra is extremely scanty. In 1872 Strasburger published an account of *Ephedra altissima* and *E. campylopoda*, dealing with the development of the microsporangiate and megasporangiate strobili. In 1879 he described stages in the development of the embryo in *E. altissima*. Jaccard ('94) described in a fragmentary way *E. helvetica*, giving most attention to spermatogenesis. He also gave some attention to fertilization and early stages of embryogeny.

The present study was undertaken with the hope of being able to follow in a fairly complete way the life-history of *E. trifurca* Torr. This account, dealing with spermatogenesis and oogenesis, is to be followed shortly by another dealing with fertilization and embryogeny.

## METHODS.

Material was collected in the vicinity of Mesilla Park, N. M., from December 20, 1902, to May 11, 1903. The second collection was made one month after the first; and as development became more rapid collections were made at intervals of four days. The strobili, attached to a short piece of the stem, were packed in wet cotton, and on reaching the laboratory four days later were placed in a moist chamber to enable them to recover turgescence. That fixation immediately after removal from the tree is not absolutely necessary is shown by nuclei in all stages of division. Further treatment did not differ essentially from approved methods of microtechnique.

### THE STAMINATE STROBILUS.

*E. trifurca* is monosporangiate, and the staminate as well as the ovulate strobili are borne in whorls around the nodes of the stem. Exceptional instances were noted in which the strobili were bisporangiate (*fig. 1*). Strasburger figures such a strobilus in *E. campylopoda*, and refers to it as an abnormal inflorescence. In another instance two ovules were present in a staminate strobilus of *E. trifurca*, although one is the usual number in the ovulate strobilus. This last, however, has many exceptions.

Shaw ('96) reports a strobilus of *Sequoia sempervirens* in which the upper part was ovulate and the lower staminate. Dickson ('60) observed the same thing in *Picea excelsa*. Coulter and Chamberlain ('01) figure strobili of Abies which are staminate at the apex and base and ovulate between. Goebel ('01) observed that in *Pinus maritima* the microsporangia were at the base of the strobilus and the megasporangia above. In the middle region he found rudimentary ovuliferous scales in the axils of the microsporophylls. In Tumboa the flowers are functionally monosporangiate, but in the center of a whorl of stamens there is a single functionless ovule with a spirally coiled micropyle. This seems to indicate that at a not remote period of its history the flowers were perfect. Ephedra, however, appears to have gone a step farther, and has become wholly monosporangiate; and the occasional bisporangiate strobili are reversions. It seems that, instead of regarding such occasional strobili as abnormal, it is better to consider them as atavistic; as pointing back to a bisporangiate

ancestry.   Atavistic tendencies should not be lightly passed over, for
it is from such reversions that we may expect valuable hints as to
previous conditions.

### THE MICROSPORANGIUM.

In the first material collected, December 20, 1902, the group of
cells which gives rise to the staminate flower is shown in *fig. 2*.   No
archesporial cells are yet distinguishable either by size or staining
reactions, nor is the beginning of the perianth visible.   Cell division
is proceeding quite rapidly, and there. is apparently considerable
activity throughout the winter months.

A month later the perianth is quite well developed (*fig. 3*).   The
cells immediately beneath the epidermis are about the same size as
the adjacent ones, and as yet no differentiation into archesporium
can be recognized.   At the base of the strobili the flowers are much
farther advanced than at the apical region.   Later in the season all
stages from rudimentary sporangia to mother-cells may be found in
the same strobilus.

*Fig. 4* shows a later stage in the development of an anther taken
from the base of a strobilus.   There is no positive evidence that the
archesporium rises from a single hypodermal cell, but such is probably
the case.   The primary wall layer divides periclinally, giving rise
to the wall layer and tapetum.   The wall-cells do not divide peri-
clinally, all divisions being anticlinal (*figs. 5, 6*).   The sporogenous
cells do not divide in any definite plane (*fig. 5*).   The stages shown
in *fig. 5* were common in basal sporangia February 9, 1903.

*Fig. 6* shows a more advanced stage of the sporangium.   The
wall layer and tapetum are completely separated, and the sporogenous
cells have ceased to divide; in fact, they are spore mother-cells which
have not yet taken on the appearance which is characteristic of older
mother-cells (February 15, 1903).   A little later the wall-cells become
flattened by the growth of the mother-cells and the tapetum.   No
further anticlinal division of the wall-cells takes place after they
begin to be flattened.   They become much stretched by the further
growth of the adjacent cells.   The tapetal cells increase in size and
stain intensely, this last because of the presence of food in large
quantities.   *Fig. 7* shows a more advanced stage.   The wall-cells are

beginning to disintegrate, the tapetal cells are increasing in size and dividing anticlinally, and the mother-cells are in the resting condition (February 15, 1903).

In gymnosperms the number of wall layers varies considerably. In Cycadales, Lang ('97) found the wall of Stangeria to consist of from three to six layers; in Ginkgoales they number from four to seven. Chamberlain ('98) found the wall of *Pinus Laricio* to be almost constantly three-layered. Coker ('02) found three wall layers in Podocarpus, the cell-walls of which are very thin and ultimately collapse; and in Taxodium he found a single layer. In *E. trifurca* the wall is a single layer of cells, and Strasburger found the same condition in the species studied by him.

In *E. trifurca* numerous instances were observed in which individual tapetal cells were not distinguishable from adjacent mother-cells. This seems to indicate that the tapetum is potentially sporogenous, and by virtue of its position has become sterile. With the appearance of the mother-cell the history of the sporophyte ends.

In general the resting stage of the microspore mother-cell in gymnosperms is long. Chamberlain ('98) observed mother-cells in *Pinus Laricio*, *Cupressus Lawsoniana*, and *Taxus baccata canadensis* in October. The reduction division occurred about May 1, thus giving a resting period of about seven months. In Ephedra the first observed reduction division was on March 12, giving a resting period of about one month.

At the time of the reduction division the cells of the wall layer are reduced to nuclei, scarcely a trace of cytoplasm being present. The cells of the tapetal layer become conspicuously vacuolated and their nuclei much enlarged. The nuclei become usually about four times the volume of those of the epidermal cells (*fig. 7*). Two or more nuclei are present in many tapetal cells at the time tetrads are formed. These last divisions appear to be amitotic, and nuclei in all stages, from the dumb-bell stage to complete separation, can be seen. At this time the tapetal cells, especially those nearest the bottom of the loculi, become enormously distended and very vacuolate (*fig. 14*). Soon afterwards they become a flattened plate and disappear.

### THE REDUCTION DIVISION AND MALE GAMETOPHYTE.

As has been said, the microspore mother-cell remains in the resting stage about one month. The mother-cells up to the late prophase are filled with starch, which now quickly disappears. There does not at all times seem to be uniformity in the stages of division in the cells of a loculus. Instances were observed in which all the cells of a loculus were in the same phase of division. Again, those in the upper part of a loculus were in synapsis, those at the bottom had formed tetrads, while all intermediate stages were between.

The spirem segments into twelve chromosomes (not all of which are shown in *fig. 8*), which as they come to lie in the equatorial plane of the nucleus are short and thick, closely massed, and can be counted only with extreme difficulty. The result of repeated countings made in various stages of the first division, as well as in the second, leaves no doubt that the gametophyte number is twelve. Jaccard reports eight in *E. helvetica.*

Twelve appears to be the prevailing number of chromosomes in the gametophytes of gymnosperms. Three exceptions to this statement are to be noted: Overton ('93) reports eight for *Ceratozamia mexicana;* Strasburger ('04) finds eight in *Taxus baccata;* the other is *E. helvetica,* with eight according to Jaccard. Dixon ('98) reported eight chromosomes for *Pinus sylvestris,* but Blackman ('98) and Miss Ferguson ('01) have shown beyond doubt that the number in this species is also twelve.

Each chromosome apparently consists of four rods lying in extremely close contact. In the heterotypic division (*fig. 9*) the chromosome divides longitudinally, the ends opening out to form the X, Y, V, and O forms which are characteristic of the heterotypic division in higher plants. A membrane (*figs. 11, 12*) begins to form between the daughter-nuclei, as if spores of the bilateral type are to result, but in the great majority of cases the membrane wholly disappears, and the spores are of the tetrahedral type; although instances were noted in which they are probably bilateral. The second division in the pollen mother-cell is homotypic (*fig. 13*) and immediately follows the heterotypic division. In this second division longitudinal splitting of the chromosomes can be seen with little difficulty. The J form is quite conspicuous. As the chromosomes separate, in

many instances they become quite irregular, being stretched almost to the point of breaking. It is quite possible that irregular numbers of chromosomes, which are occasionally reported in plants, may have originated by the breaking of an individual chromosome. The microspores, still within the wall of the mother-cell, quickly assume an oval form (*fig. 14*).

After a brief period of rest (*fig. 15*) the nucleus of the microspore divides, and the first prothallial cell is formed. It has been determined beyond a reasonable doubt that a wall is laid down between the two nuclei (*figs. 16, 17*), although it is extremely difficult to differentiate. The prothallial cell is pressed closely against the end of the microspore by the growth of the other cell, its nucleus usually taking the meniscus form (*figs. 17–22*). The other cell, still remaining at the center of the spore, enlarges, and dividing (*fig. 17*) gives rise to the second prothallial cell and the antheridium initial (*fig. 18*). The antheridium initial does not appear to be separated from the second prothallial cell by a wall, but both nuclei remain in the same mass of cytoplasm which originally surrounded the nucleus before division (*fig. 18*). Here again arises a great difficulty in making conclusive observations. It may be that a wall is laid down and almost immediately resorbed, as Juel ('oo) has shown to be the case in tetrad formation in *Carex acuta*, where a cell plate is formed and immediately resorbed, leaving the tetrad nuclei free within the wall of the mother-cell. It is conceivable that such a wall may be laid down, for it must be remembered that the entire prothallial region of gymnosperms is undergoing modification, in that the prothallial cells are either more or less ephemeral or altogether wanting; and that when cells are becoming obsolescent the wall is the first to disappear, leaving the two nuclei free within the common cytoplasm; next, the nucleus occasionally fails to divide; and finally no division takes place at all.

The second prothallial cell becomes flattened because of pressure due to the growth of the antheridium initial, and its nucleus becomes plano-convex or even meniscus-shaped, with its plane or concave face turned toward the first prothallial cell (*figs. 18, 20*). The nucleus of the antheridial cell, still at the center of the microspore, enlarges very much (*fig. 18*) and divides (*fig. 19*), giving rise to the generative

cell and the tube nucleus (*fig. 20*).  The tube nucleus, although
lying in close proximity to the wall of the microspore, does not become
flattened as do the prothallial cells.  In all preparations examined
there seems to be no break in the cytoplasm surrounding the tube
nucleus and the second prothallial cell (*figs. 20–22*), nor is a wall
laid down between the tube nucleus and the primary spermatogenous
cell.  The primary spermatogenous cell—or generative cell—lies in
a mass of cytoplasm differentiated from the surrounding cytoplasm
by a slightly denser zone (*figs. 20, 21*).  This condition of affairs is
doubtless comparable to that of the generative cell of angiosperms,
where there is a well-defined *Hautschicht*, on the outside of which
food material is conspicuous.  The primary spermatogenous cell
dividing (*fig. 21*) gives rise to the stalk cell and the body cell, both
of which lie within the cytoplasmic ring previously mentioned as
surrounding the primary spermatogenous cell.  The male gameto-
phyte at this time (April 1, 1903) contains five nuclei: two prothallial
cells, tube nucleus, stalk cell, and body cell.  The microspore will
be shed ten to fifteen days later.

The time periods in the development of the strobilus and male
gametophyte are as follows: The strobilus appeared the previous
season; on December 20, 1902, the group of cells which gives rise to
the staminate flower is apparent, but the "perianth" is not yet visible;
January 27, 1903, the "perianth" is well along and the primordia
of the sporangia are clearly apparent; February 10, the primary
wall cells are dividing; by February 15 many sporangia have mother-
cells in the resting condition; one month later (March 15) the reduc-
tion division takes place; by April 1 the spores are mature, and about
April 15 the pollen is shed.  These records are for one season only,
and the periods may be expected to vary somewhat in other seasons,
the variations being of course dependent on various external factors.

It appears that Jaccard never saw the prothallial cells, for he
says that at maturity the pollen grain contains three nuclei: "a
large central nucleus representing the antheridial cell of Belajeff and of
Strasburger; and two vegetative polar nuclei, of which one is the tube
nucleus (*noyau du tube pollinique, Pollenschlauchkern*), and the other
homologous with the *Stielzelle* of the German authors."  So, putting
this into present terminology, what he saw at the shedding of the pollen

were tube nucleus, stalk cell, and body cell. It is hardly to be expected that two prothallial cells will be present in one species and wholly absent in another.

The number of prothallial cells varies in gymnosperms. Those in which two have been reported are *Ginkgo*, Strasburger ('92); *Larix europaea*, Strasburger ('84); *Picea vulgaris*, Belajeff ('93); *Pinus Laricio*, Coulter and Chamberlain ('01); *Podocarpus coriacea*, Coker ('02); *Ceratozamia longijolia*, Juranyi ('82), sometimes two, but more often one. Those in which one has been reported are *Ceratozamia*, Juranyi ('82); *Zamia*, Webber ('97); *Cycas*, Ikeno ('98); *Ephedra campylopoda*, Strasburger ('72). No prothallial cells have been observed in *Biota*, *Cupressus*, and *Juniperus*, Strasburger ('92); *Taxus baccata*, *Juniperus*, Belajeff ('93); *Thuja occidentalis*, Land ('02); *Taxodium distichum*, Coker ('03); *Cupressus* (4 spp.), *Taxus baccata* and 4 vars., *Juniperus* (2 spp.), *Chamaecyparis* (5 spp.), *Callitris*, *Cryptomeria japonica*, and *Thuja orientalis*, Coker ('04); *Ephedra helvetica*, Jaccard ('94).

It is quite probable that in many gymnosperms two prothallial cells will be found eventually, and probably one at least will be found in some of those forms where up to the present none have been demonstrated.

### THE OVULATE STROBILUS.

The ovulate strobilus was first collected in December. It differs in external appearance from the staminate strobilus in that it is longer and more slender.

The ovulate flower is not differentiated as early as is the staminate. On March 1, 1903, traces of the outer and inner integuments could be seen; a few days later the integuments presented the appearance shown in *fig. 23*. Much has been said concerning these integuments or perianths, as they are variously called. Transverse sections at different levels (*figs. 24, 25*) show that the outer integument results from a fusion of four leaves, and the inner integument from a fusion of two leaves. The outer integument becomes several cells thick, and in later stages quite hard. The inner integument is never more than two cells thick. A short time before the pollen is shed, the inner integument rapidly elongates and thrusts itself out through the apex of the strobilus. The exposed end is wide open, and is also

slit a short distance down one side (*fig. 44*). The pollen enters the open end of the integument, and drops down to the bottom of the pollen chamber (*fig. 44*), where it lies in contact with the archegonial end of the female gametophyte. So far as known, there is no other gymnosperm in which the pollen grain is placed so near the archegonia.

The archesporium could not be traced definitely back to a single hypodermal cell, but there are indications that such may be its origin. The earliest stage in which a suggestion of differentiation was observed is shown in *fig. 26*, March 8, 1903. The lower larger cell in this figure is beyond doubt the megaspore mother-cell. The large cell above will divide again and again, and thus place the megaspore mother-cell deeply within the nucellus. In *fig. 27* the divisions of a similar cell are clearly apparent, and the conspicuous megaspore mother-cell is shown. In general not more than one megaspore mother-cell is organized, but instances were noted in which two and very rarely three mother-cells were present. Sometimes, but not always, each of these cells produce megaspores. In general one mother-cell soon gains an advantage over the others and causes their rapid disintegration.

The mother-cell grows rapidly, meanwhile encroaching on the surrounding nucellar tissue. The reduction division occurred about March 8, 1903 (*fig. 28*). The second division quickly follows the first, and the more deeply placed megaspore alone functions. According to both Strasburger and Jaccard, three megaspores only are produced in the forms studied by them. In *E. trifurca* either three or four may occur (*figs. 29, 30*). In many instances the upper cell does not divide; again, the division may be incomplete, or it may be completed entirely. In no observed instance does the division of the upper cell take place until two lower megaspores are entirely separated; *fig. 29* shows such a late division of the upper cell. It seems that the more deeply placed cell because of its relation to the food supply is enabled to divide first. From this it follows that the most favorably placed megaspore—the lower one—is enabled to grow so rapidly as to preclude much further development on the part of the others. The megaspore remains a very short time in the resting condition. The number of chromosomes at the reduction division is

twelve, thus confirming the observations made on the microspore series.

Lang ('97) has shown that in Stangeria the mother-cell forms a row of three megaspores; Treub ('81) reports the same for Ceratozamia; and three are reported for Ginkgo. Among the Coniferales four are frequent. In *Pinus Laricio* I have observed that either three or four are formed indifferently. Strasburger ('79) gives three as the usual number in Taxus, although four frequently occur; in his later work on *Taxus baccata* (04') he says that four cells are formed from the megaspore mother-cell. Juel ('00) finds four in *Abies sibirica* and *Larix sibirica;* Shaw ('96) reports four in Sequoia; Lawson ('04) studying the same species of Sequoia finds three; Coker ('03) finds three in *Taxodium distichum* and ('04) four in *Thuja orientalis*, where they are not arranged in a row, but in nearly regular tetrad form. Strasburger finds three in *Ephedra campylopoda*, and Jaccard three in *E. helvetica;* in *E. trifurca* three or four are formed indifferently, dependent on the rapidity with which the functioning megaspore encroaches. This encroachment is probably the reason for the differences reported in the forms mentioned above.

### THE FEMALE GAMETOPHYTE.

The two nuclei resulting from the division of the megaspore seem invariably to take the position with reference to the major axis of the ovule shown in *fig. 31*, for in no observed instance did the nuclear plate vary from this position. Before the spindle fibers and cell-plate have disappeared, a ring-like vacuole appears, entirely surrounding the cell-plate. The rapid increase in size of this vacuole is one of the chief factors concerned in the parietal placing of the free nuclei. These two nuclei divide simultaneously, and the resulting four take equidistant positions at the periphery of the embryo sac (*fig. 32*). Successive simultaneous divisions (*figs. 33, 35*) rapidly follow each other until the maximum number of nuclei is reached, which in the present instance apparently does not exceed 256. It may be of interest to note that at only one time—immediately after the division of the megaspore—is the vacuole free from cytoplasm. Careful staining shows that at all later stages (*figs. 32–35*) it is filled with a delicate cytoplasmic structure, which gradually increases in density until free nuclear division ceases, which was about April 1,

1903. Free nuclear division, therefore, extends through a period of approximately twenty days.

Simultaneously with the appearance of walls, the gametophyte is differentiated into two distinct regions: a micropylar or sex-organ producing region, and an antipodal or nutritive region. The behavior of the lower part of the gametophyte is strongly suggestive of the same region in *Gnetum Gnemon*, as described by Lotsy ('99). The cells of the antipodal region are only slightly elongated and are fairly regular in outline. As growth proceeds—and it is very rapid—this lower part is again separated into two physiologically distinct regions: storage and haustorial. The storage region comprises the greater part of the gametophyte, and is highly charged with starch and other foods. In the center are a few rows of thin-walled cells containing much more food than the surrounding cells, and extending up to the base of the archegonia. It is down through this thin-walled region that the embryo is thrust by the elongation of the suspensor. The haustorial part of the gametophyte (*fig. 44*) is composed of one or two layers of the outermost cells, which are clearly haustorial in function. Those at the tip of the gametophyte are elongated to a point ending in a single cell. The haustorial cells do not have the great elongation shown by the cells in the same region of Zamia. The storage and haustorial region increases in size as long as the embryo continues to grow.

The region in the immediate vicinity of the archegonia and for some distance below is very loosely organized, and the cell-walls are extremely delicate. In the central region immediately beneath the archegonia instances were noted in which the walls were late in appearing. The cells of this region are very vacuolate, and in consequence have little contents.

This feebly organized region is significant from a phylogenetic standpoint. In Tumboa the upper part of the gametophyte is loosely organized, and the numerous cells which function as eggs never get beyond the archegonium initial stage. In *Gnetum Gnemon* the same region never gets beyond the free nuclear stage, and these free nuclei function directly as eggs. It is possible that Ephedra, Tumboa, and Gnetum show stages through which the ancestral forms of angiosperms in all probability passed.

## THE ARCHEGONIUM.

About April 1, 1903, the archegonium initials were first observed. They are the pyramidal form common to most gymnosperms. Two is the usual number, one is occasional, and three are rare. The primary neck-cell is quickly cut off after the initial becomes apparent (*fig. 36*), and almost immediately divides periclinally (*fig. 37*). Other periclinal walls follow (*fig. 40*), sometimes as many as four or five tiers being cut off before anticlinal walls appear; and as many as eight tiers of neck cells have been observed. Each tier divides anticlinally into four cells; later there may be six or eight in a tier, also the walls which come in later are no longer truly periclinal, thus giving the neck a somewhat irregular appearance (*fig. 41*). Thirty-two is probably the minimum number of cells, but it may go much higher. *Fig. 39* shows a cross section of the neck 40 $\mu$ above the top of the central cell. Of all gymnosperms Ephedra has the longest-necked archegonium. This may be due to the fact that the archegonial end of the gametophyte is freely exposed to the air.

Simultaneously with the appearance of the archegonium initials, a change is observable in the nucellus. Traces of disorganization become visible at the tip of the nucellus and gradually proceed downward, so that by the time the ventral nucleus is cut off, the cells at the apex of the nucellus have completely disappeared, leaving a pollen-chamber shaped like the frustrum of an inverted cone. The pollen-grains are thus enabled to come in direct contact with the gametophyte and the necks of the archegonia. So far as has been reported, Ephedra is the only gymnosperm having any part of the gametophyte exposed freely to the air, except in the case of *Cycas circinalis*, where, according to Warming ('77), if fertilization does not occur, the gametophyte continues to grow, ultimately bursting out through the micropyle and developing chlorophyll on exposure to light. Strasburger's figures show a pollen-chamber in *E. altissima*, but not in *E. campylopoda;* and Jaccard finds one present in *E. helvetica*. In Cycadales and Ginkgoales the pollen-chamber, formed by disintegration of the cells of the nucellar beak, is a conspicuous feature. In *Pinus Laricio* it is so small as to escape notice in most instances, while in *Thuja occidentalis* the tip of the nucellus at the time of pollination is an expanded stigma-like surface.

The nucleus of the central cell lies in close proximity to the neck of the archegonium. As the central cell enlarges, it does not have a conspicuous vacuole in the center, like Pinus and the Cupressineae, but is almost completely filled with cytoplasm except in the immediate vicinity of the nucleus, where there are a few small vacuoles. Later the cytoplasm in the lower part of the archegonium becomes almost homogeneous. A conspicuous kinoplasmic mass lies at a little distance below the nucleus (*fig. 41*). In the earliest stages it is coarsely granular, and later becomes dense, and is larger and sharper in outline than the similar body which is so conspicuous in some of the pines and in *Thuja occidentalis*.

When two or three archegonia are present, one is usually smaller than the others, as is shown in *fig. 38* (a cross-section through the middle region of the archegonia). When one archegonium is present it is very large as compared with the larger of two in a gametophyte. It is questionable if the eggs in the smaller archegonia regularly function.

The jacket-cells are at first rectangular, with the longer axis at right angles to the long axis of the central cell (*fig. 40*). Since periclinal division does not keep pace with the elongation of the central cell, the jacket-cells become much elongated (*fig. 41*). Their walls, never at any time thick, become so tenuous that they can scarcely be seen, and evidently offer little resistance to the passage of food into the central cell. There is evidence that at the time of fertilization the walls separating them from the egg break down altogether. *Fig. 41* shows two archegonia at the time of pollination (April 15, 1903).

The ventral nucleus was cut off about April 15 in the season of 1903. In material collected during the season of 1904 from the same plants, the ventral nucleus was cut off about April 1. This difference is probably due to the fact that the season of 1904 was unprecedentedly hot and dry.

No trace of a wall can be seen between the ventral nucleus and the egg, although in some instances there is a suggestion of cytoplasmic thickening between the two nuclei. The cytoplasm at the upper end of the central cell is still quite vacuolate; in the lower part it has now become very dense, in fact almost homogeneous.

The ventral nucleus remains in the upper part of the archegonium, and enlarging (*fig. 42*) becomes very conspicuous. The egg nucleus passes to the center of the archegonium, enlarges, and surrounds itself with a mass of cytoplasm, slightly different from that farther away from the nucleus in that it at first consists of radial strands proceeding out from the nucleus in all directions. A thickening of the cytoplasm next appears all around the nucleus at the place where the radiations meet the general cytoplasm of the archegonium. This thickening is very pronounced in most instances, again it can be seen with difficulty; it very much resembles the first appearance of the membrane around the egg and synergids of angiosperms.

### SUMMARY.

*Ephedra trifurca* is monosporangiate, but bisporangiate strobili occasionally occur.

The beginnings of the staminate flower were clearly apparent in December, and the pollen was shed about the middle of April, the interval being thus a little over four months.

The anthers develop in acropetal succession on a strobilus, and are surrounded by a perianth.

Microspore mother-cells were observed about the middle of February, and the reduction division occurs about one month later.

The gametophyte number of chromosomes is twelve.

There are two persistent prothallial cells; the first is cut off by a wall; the second is not cut off by a wall.

The primary spermatogenous cell surrounds itself by a membrane (*Hautschicht?*), and on the division of the primary spermatogenous cell, the stalk cell and body cell continue to be surrounded by this membrane, and are not separated from each other by a wall.

The only wall formed in the pollen grain is the one which cuts off the first prothallial cell.

The male gametophyte at the time of shedding consists of two prothallial cells, stalk cell, body cell, and tube nucleus.

The megasporangium is surrounded by two integuments, the outer of which consists of four fused leaves; the inner of two fused leaves.

The megaspore mother-cell is deeply placed within the nucellus

and gives rise to either three or four megaspores arranged in a row, the most deeply placed megaspore being functional.

The nuclei resulting from the division of the megaspore show polarity in that they are definitely oriented with respect to the axis of the megasporangium.

A vacuole appears between the nuclei resulting from the division of the megaspore before the spindle has disappeared, and soon becomes filled with delicate cytoplasmic structures which increase in density until walls appear.

The free nuclei are parietally placed from the beginning, divide simultaneously, and are presumably 256 in number before walls appear.

The female gametophyte is separated into two regions: a loosely formed archegonial region, and a more compact antipodal region, the latter being composed of a haustorial and a storage region.

The archegonia vary from one to three, two being the usual number; the neck is composed usually of eight tiers of cells; and there are no archegonial chambers.

The apex of the nucellus breaks down, and a conspicuous pollen-chamber is formed. The necks of the archegonia are thus exposed to the air, and the microspores are brought directly into contact with the female gametophyte.

No wall is formed between the ventral nucleus and the egg; the former becomes quite large and takes a position a short distance below the neck of the archegonium.

The egg takes a position midway in the cytoplasm of the archegonium, surrounds itself with a membrane comparable to the one which invests the eggs of angiosperms, and in this position awaits fertilization.

At the time of fertilization the cytoplasm in the archegonium has become almost homogeneous and very dense, except in the region immediately below the neck of the archegonium, where it is loosely vacuolate.

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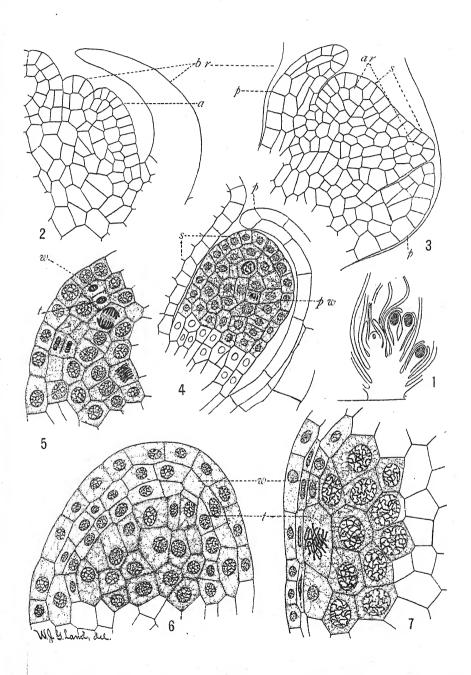
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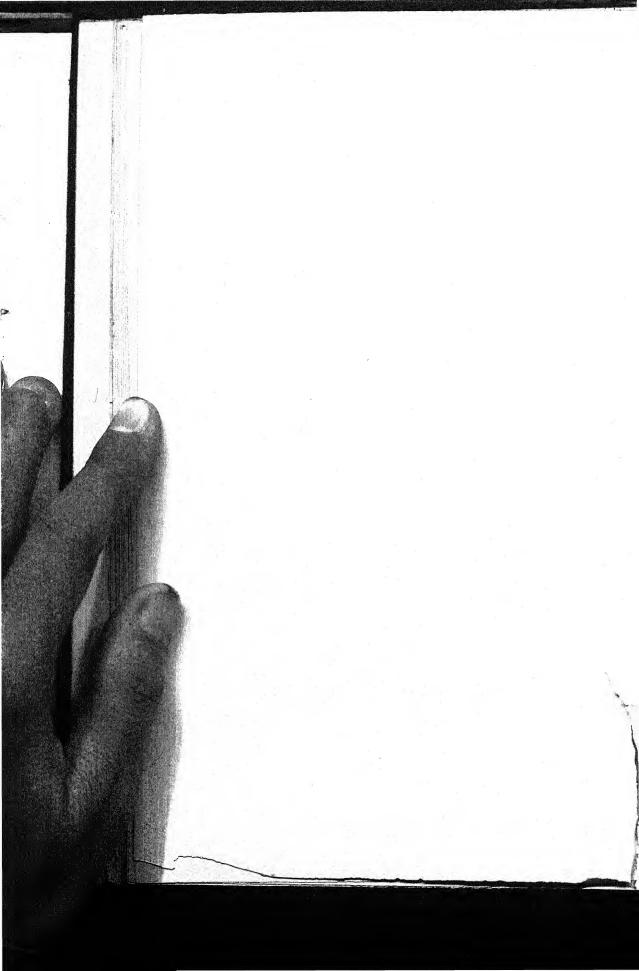
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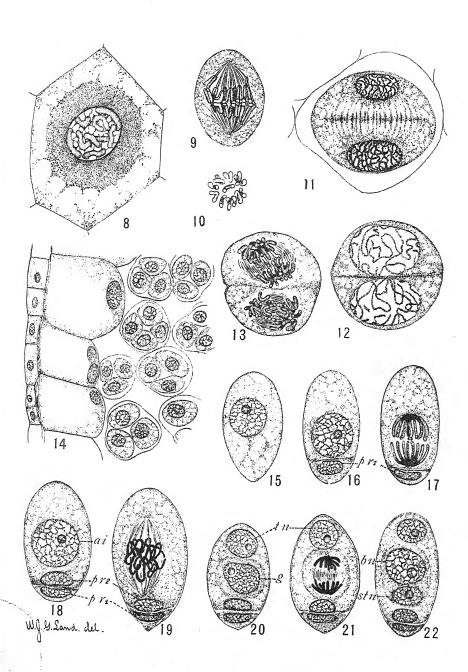
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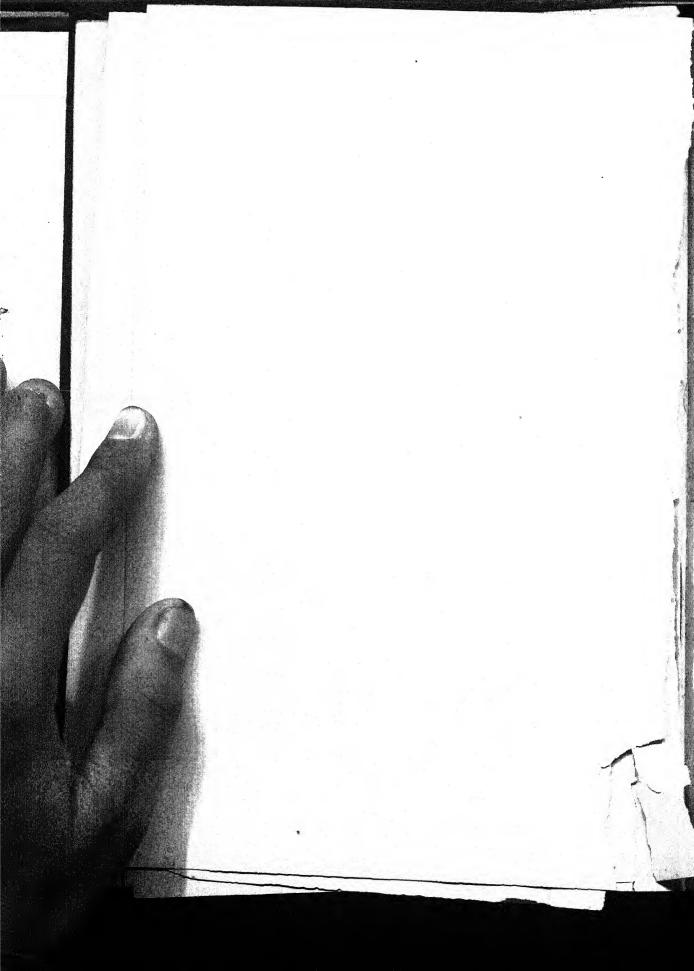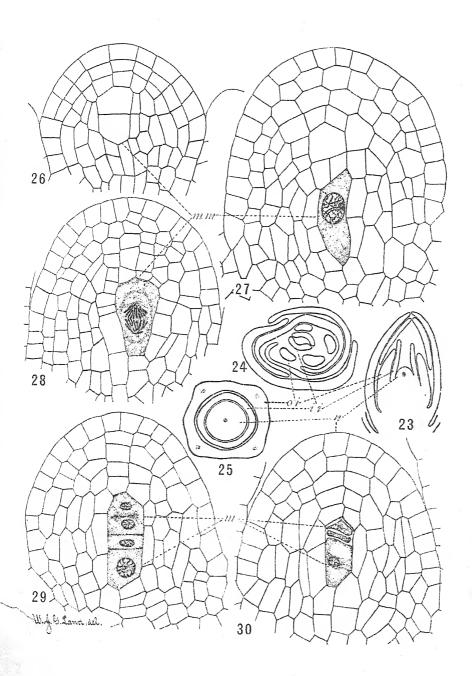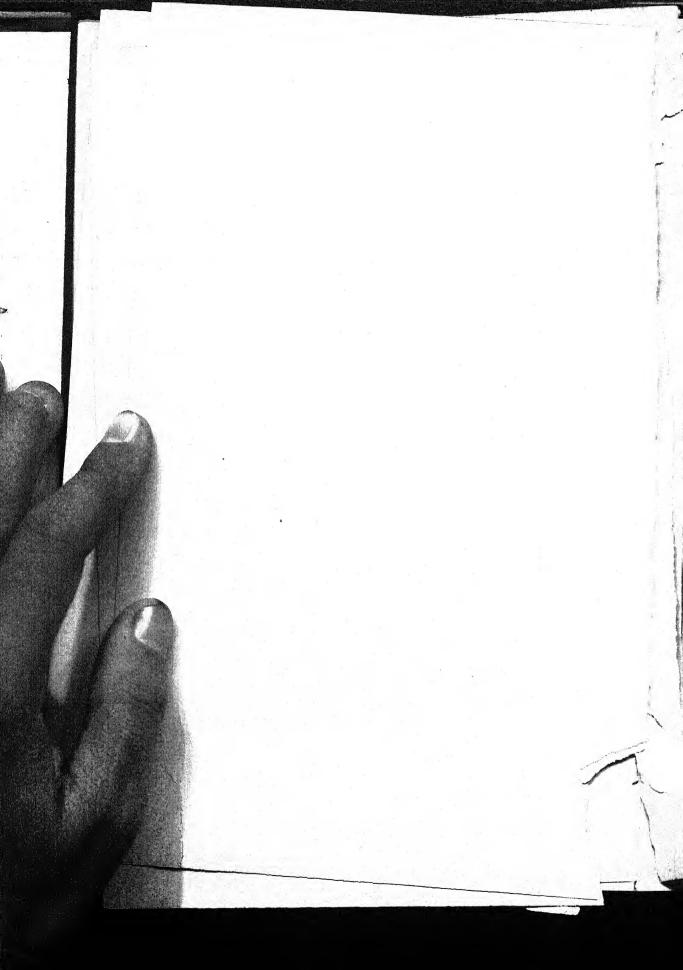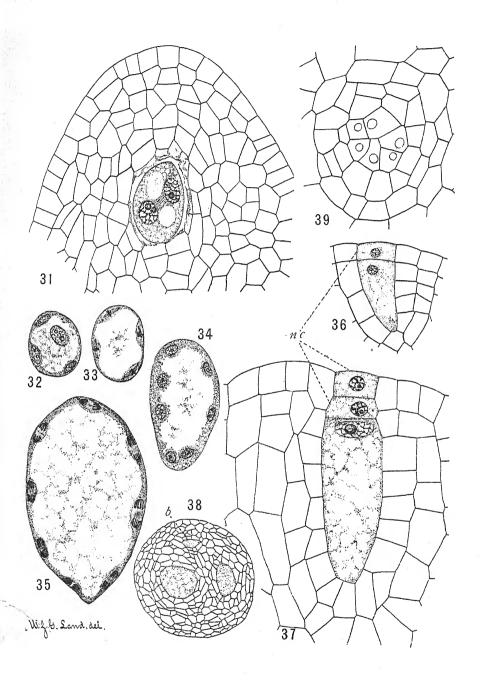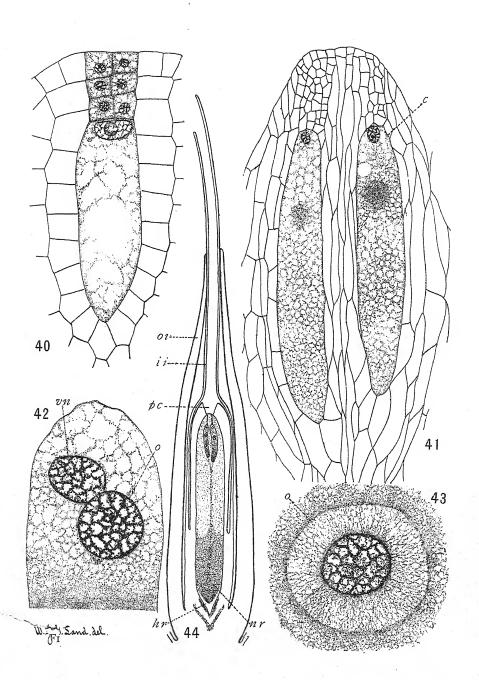
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## EXPLANATION OF PLATES I–V.

All figures were drawn with an Abbé camera lucida, and reduced one-half in reproduction. Abbreviations are: *br*, bract; *a*, primordium of stamen; *p*, perianth; *oi*, outer integument; *ii*, inner integument; *n*, nucellus; *pc*, pollen-chamber; *s*, microsporangium; *pw*, primary wall-cells; *w*, wall-cells; *t*, tapetum; *ar*, archesporial cells; *pr¹*, first prothallial cell; *pr²*, second prothallial cell; *ai*, antheridium initial; *tn*, tube nucleus; *g*, primary spermatogenous cell; *stn*, nucleus of stalk cell; *bn*, nucleus of body cell; *mm*, megaspore mother-cell; *m*, megaspores; *nr*, nutritive region of female gametophyte; *hr*, haustorial region of gametophyte; *b*, abortive archegonium; *nc*, neck cells; *c*, central cell; *vn*, ventral nucleus; *o*, egg.

FIG. 1. A bisporangiate strobilus. × 16.

FIG. 2. Portion of a longitudinal section through a staminate strobilus showing bracts and primordia of two anthers. × 225.

FIG. 3. Longitudinal section through an anther showing beginning of perianth and primordia of two sporangia. × 225.

FIG. 4. Longitudinal section through a sporangium showing sporogenous cells, part of an adjoining sporangium, and perianth × 225.

FIG. 5. Division of primary wall cells; the sporogenous cells are also actively dividing. × 500.

FIG. 6. Early stage of the microspore mother-cells. × 500.

FIG. 7. Microspore mother-cells in resting stage. × 500.

FIG. 8. Microspore mother-cell after segmentation of the spirem. ×1500.

FIG. 9. Microspore mother-cell, heterotypic division. × 1500.

FIG. 10. Polar view of chromosomes in anaphase of second mitosis in microspore mother-cell. × 1500.

FIG. 11. Later stage in division of microspore mother-cell. × 1500.

FIG. 12. Prophase of homotypic division. × 1500.

FIG. 13. Homotypic division. × 1500.

FIG. 14. Tetrads and enlarged tapetal cells. × 500.

FIG. 15. A microspore shortly before the first division. × 1500.

FIG. 16. Microspore after formation of first prothallial cell. × 1500.

FIG. 17. Division to form second prothallial cell and antheridium initial. × 1500.

FIG. 18. First and second prothallial cells and antheridium initial. × 1500.

FIG. 19. Division of antheridium initial. × 1500.

FIG. 20. Two prothallial cells, primary spermatogenous cell, and tube nucleus. × 1500.

FIG. 21. Division of primary spermatogenous cell. × 1500.

FIG. 22. The two prothallial cells, stalk cell, body cell, and tube nucleus. × 1500.

FIG. 23. Median longitudinal section through a megasporangiate strobilus showing the two integuments and nucellus with gametophyte. × 46.

FIG. 24. Section through the strobilus above the nucellus showing the four parts of the outer integument and the two parts of the inner integument which later become tubes. × 46.

FIG. 25. Section through the strobilus at level of gametophyte, showing the fused parts. × 46.

FIG. 26. Megaspore mother-cell becoming differentiated. × 500.

FIG. 27. Megaspore mother-cell, resting stage. × 500.

FIG. 28. Megaspore mother-cell dividing. × 500.

FIG. 29. A row of four megaspores, showing late division of upper daughter nucleus. × 500.

FIG. 30. A row of three megaspores; the upper daughter-nucleus has failed to divide. × 500.

FIG. 31. First division of the megaspore, showing formation of the central vacuole. × 500.

FIG. 32. Four-celled stage of female gametophyte. × 500.

FIG. 33. Simultaneous division of the nuclei; eight-celled stage. × 500.

FIG. 34. Female gametophyte; sixteen cells. × 500.

FIG. 35. Female gametophyte; simultaneous division to form sixty-four free nuclei. × 500.

FIG. 36. Archegonium with primary neck cell and central cell. × 500.

FIG. 37. Archegonium showing the enlarged central cell and two neck cells. × 500.

FIG. 38. Transverse section of gametophyte at level of central cell, showing a large, a small, and an abortive archegonium. × 75.

FIG. 39. Transverse section through neck of an archegonium at a distance of 40 μ above the central cell. × 500.

FIG. 40. An archegonium slightly older than *fig. 37*. × 500.

FIG. 41. Two archegonia just before the division of the nucleus of the central cell. × 112.

FIG. 42. Egg nucleus and ventral nucleus lying in the upper part of the archegonium. × 500.

FIG. 43. Egg lying near the center of archegonium and surrounded by a membrane of thickened cytoplasm, and ready for fertilization. × 500.

FIG. 44. Longitudinal median section through the ovule and integuments, showing reproductive, storage, and haustorial regions of the gametophyte. × 48.

# THE WATER-RELATION OF PUCCINIA ASPARAGI.

## A CONTRIBUTION TO THE BIOLOGY OF A PARASITIC FUNGUS.

RALPH E. SMITH.

(WITH TWENTY-ONE FIGURES)

WHETHER the use of the term "ecology" would be consistent and proper throughout the present article, the writer must confess his inability to decide. With plants of independent existence ecology has become a well-defined branch of botanical science, but when complicated with the phenomena of parasitism there must be distinguished two fairly distinct classes of life-relations; those which act upon the parasitic organism directly, and those which affect it, even more decidedly perhaps, in a secondary or indirect manner through their effects upon the host-plant. "Biology," in the European sense, seems on the whole a more fitting term for the present purpose; since at many points it is difficult to say whether we are considering the relation of the parasite to its environment, or to its host's environment, or whether its host is its environment. The subject is one of ecology in the broadest sense, yet a distinction must be made between the relations of an organism to natural influences, and its relations to the effects of perhaps the same influences upon another organism upon which it lives as a parasite. The fungus has no soil-relation, of course, but its connection with the host-plant is much more than this, though corresponding to a certain extent. Without extended discussion on this point, it will suffice to say that it has seemed to the writer very desirable to establish upon a systematic basis the relations existing between parasitic fungi in general and the various influences exerted upon them in nature, either directly or acting through ·the medium of the host-plant. While many scattered observations of this kind exist, very little definite work has been done in establishing general principles or in drawing definite conclusions. ·The observations contained herein are offered as a modest contribution in this direction.

It is well established in a general way that the development of

those fungi that live upon higher plants is favored by wet weather. This is so universally the case that we may almost conclude without further consideration that under normal conditions the water-relation of such parasites is of more importance in their development than any
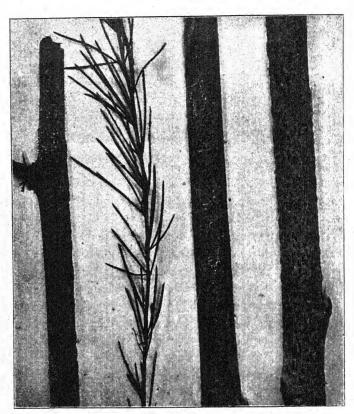


FIG. 1.—Asparagus rust, *Puccinia Asparagi* DC., in all stages. Milpitas, Calif., July 4, 1903.

other condition. Considering this as established, there still remains a broad field for research in determining just why this is true, and in general in analyzing the conditions and their results. This has been the writer's object in the case of the destructive parasite *Puccinia Asparagi* DC., which has proved especially favorable for such study.

The asparagus rust is caused by one of the Uredineae of the sub-division *Auteupuccinia* of Schroeter's classification; that is, the spermogonia, aecidia, uredospores, and teleutospores all develop upon the same plant. This is shown in *fig. 1*, where the various spore forms may be readily recognized. Upon the stalks represented at the extreme right and left all four forms are present at once. This disease has long been known in Europe, but attained no prominence in this country until the fall of 1896, since which time it has spread entirely across the continent from Massachusetts to California, with extremely disastrous results to the asparagus industry.

The development of this rust is practically the same as that of others of the same class, the spermogonia and aecidia appearing in spring, followed by the uredo stage in summer, after which the teleuto or black rust appears. The development of the aecidial stage has varied, according to the writer's observation, with the nature of the spring climate in various sections of the country. In Massachusetts, where the spring is comparatively late and short, the aecidium of *Puccinia Asparagi* is not unknown, but is by no means common, and the development of this stage of the rust is decidedly limited. Going south to Long Island and New Jersey, the spring form is common, but by no means noticeable; while in California the "spring rust" is almost as well known to asparagus-growers as the later stages, and upon old beds, volunteer growth, or beds too young for cutting, it reaches a development quite unknown in the east, sometimes covering the main stalk and branches of the plant completely and causing considerable damage. *Fig. 2* illustrates a case of



FIG. 2.—Aecidial development of the rust as seen in California. Bouldin Island, April 29. 1903.

this sort.   The uredo and teleuto stages follow in order as the season progresses, and while the simultaneous occurrence of these forms is by no means unknown, it is usual, as with most similar rusts, for the uredo stage to develop almost exclusively during the summer, when the plants are most active, followed by a pure teleuto growth upon the dead stalks in fall.   The latter stage in all the Eupuccinia group is regarded, therefore, as typically the fall rust, and as a form which develops to any extent only in the latter part of the season as a result of the approach of winter and the death of the host-plant.

The relation of the development of the asparagus rust to soil and atmospheric moisture has received some attention in previous publications.   Stone and Smith[1] found a decided difference in the prevalence of the disease according to the moisture-retaining properties of the soil, the trouble being worse upon the drier soils.   So marked was this difference in Massachusetts that in regions equally exposed to infection, and in fact equally affected with the teleuto stage in the fall, the beds upon heavier, moist soils did not show, and have never shown, any rust previous to September (when the plants mature in that climate); while those upon light dry soils became badly affected with the uredo stage early in the season.   The difference not only appeared in different sections of the state in the same season, but also in the whole state in different seasons, the amount of rust in the most affected localities varying as the season was wet or dry, being least in the wet seasons.   Although not universally accepted at first, this idea has received much support from subsequent experience over practically the whole country.

In most of the large asparagus regions of the eastern states but little difference exists between the soils of the various plantations, the characteristic soil being of a light, sandy, dry nature.   In the first violent epidemic of the rust everything was affected in such sections, and differences in soil, as well as in varieties of asparagus and other factors now recognized by all, were overlooked or imperceptible. A tour of these districts at present, however, will convince the most skeptical that of the original beds those few which now remain are almost entirely upon the heavier soils, and of the new beds the most

[1] Bulletin 61, and Ann. Reports 12, 14, 15, Hatch Exper. Station of Mass. Agric. College.

thrifty are likewise on the heavier soils, other things being even approximately equal. Most of the growers in the large eastern asparagus districts recognize this, and likewise attribute the marked freedom from rust of the past two seasons to the very unusual rainfall, which fact is in itself strong evidence of the unfavorable effect of abundant soil moisture upon the fungus.

This is, of course, contrary to the established principle above mentioned that such parasites are greatly favored by wet seasons. One of the most prominent features in the observations of Stone and Smith was the occurrence in the asparagus beds least affected of the teleuto stage alone coming on at the usual time, but not preceded by any trace of the other stages, so far as could be found by thorough search. These beds were, as just mentioned, upon soils of high water-retaining capacity. Furthermore, as brought out by two extreme seasons, in a very dry summer (1897) the uredo stage appeared upon some beds which never showed it before or since, while in a season of excessive rainfall (1898) some of the places most affected with red rust in other years had only the teleutospores late in the season.

These facts were regarded as showing the indirect relation of the rust fungus to water. In the dry seasons and upon the drier soils lack of moisture unquestionably reduced the vitality of the asparagus plants. Consequently, they became more susceptible to disease and suffered in inverse proportion to the amount of soil moisture available. As to the direct relation of the parasite to water, the conclusion must be drawn from the observations of these investigators that the host-plant, depending upon the soil, felt the effects of unusual dryness to a more serious extent than did the parasite, thus turning the balance more strongly in favor of the latter; while, on the other hand, in a wet season or heavy soil the asparagus derived more benefit from such conditions than did the fungus, and thus the activity of the latter was checked. In other words, the fungus appeared to obtain sufficient moisture for its requirements even in the dry season, and received no proportionate invigoration from an excess of moisture in seasons of abundant rainfall. It is also indicated by these observations that the uredo stage is characteristic of conditions favorable to the fungus, while in the unfavorable seasons or localities no develop-

ment of the parasite took place until the plants began their natural loss of vitality at maturity, and under these conditions, when little nourishment was left for an active parasite, only teleutospores appeared.

Another side of the relation of *Puccinia Asparagi* to water was brought out particularly by Sirrine,[2] who, from his observations in New York, was led to conclude that the relation of the rust to atmospheric moisture in the form of dew or fog was the most important factor of this nature in the development of the disease. In the cases described by this writer the progress of the fungus seemed to be accelerated by excessive dew-fall, while with the absence of the latter the rust was less prevalent. In an asparagus bed upon a sloping hillside, for instance, the most rusty portion was at the base, decreasing with the rising grade. It has also been frequently observed that asparagus growing in the shade, as where a tree stands in the midst of a bed, remains free from rust when all about it is dead with the disease. This fact shows certainly that the protection thus afforded prevents infection by the fungus, and can be explained only on the ground of the prevention of dew being deposited. Stone and Smith maintained, however, that under ordinary conditions no such differences existed in their section as were observed by Sirrine, since some of the least rusted beds were in regions most subject to heavy dews, and in the case of asparagus growing on a slope, that at the bottom was likely to be least affected, on account of the usually heavier soil there. They held in regard to the influence of dew that, "when plants are not resistant enough to stand uredospore infection, it is not difficult to understand how this might take place, but the presence of any amount of dew fails to infect some beds in this state;" the beds referred to being those in heavier soil.

In the writer's opinion both of these theories as to soil and atmospheric moisture were correct, but modified by local conditions. In Massachusetts asparagus is grown upon a great variety of soils and showed from the first more decided differences in susceptibility to the rust than in any other section. These conditions were studied with great thoroughness by field observation and mechanical analysis of soils all over the state, and the conclusions arrived at have been

[2] Bulletin 188, N. Y. (Geneva) Exper. Station.

repeatedly verified from year to year. In New York and New Jersey large asparagus districts exist of practically uniform soil and of the nature characterized by the Massachusetts investigators as most favorable to rust. In these districts the disease became exceedingly virulent at first and completely exterminated the original beds, without regard to slight differences in soil or other features which are well marked in the new plantations of the same districts, now that the severity of the attack has somewhat subsided. Since dew is necessary for infection, it is but natural that where other conditions were equal, the progress of the disease should be temporarily marked by varying amounts of atmospheric moisture, but it must be said that throughout the eastern states dew is so generally abundant, even in the driest seasons, that nothing of permanent value can be credited to this relation. That dew is absolutely necessary to the development of the fungus seems proved from the effects of tree shade in asparagus fields, and this is the direct water-relation of this parasite.

Conditions in California with respect to soil and atmospheric moisture are totally different from those of any eastern state. On account of the long, rainless summers, marked differences in the natural conditions of various parts of the state, and the prevalence of irrigation, any question having to do with moisture problems can be followed with a degree of precision quite impossible under the natural conditions of the east. This refers particularly to the degree of dryness obtainable, both of soil and atmosphere, a degree approximated nowhere else in the country save in the adjoining semi-arid states. The principal asparagus-growing section of California has proved to be especially well-adapted to a study such as that herein described, and a description of this portion of the state must be given at this point.

If in the accompanying map (*fig. 3*) a triangle be imagined between the cities of Sacramento, Stockton, and Antioch, it will include, at a safe estimate, 5000 acres of asparagus. This country is at the confluence of the two great rivers of California, the Sacramento and the San Joaquin, together with a smaller stream, the Mokelumne, which enters the angle formed by the other two where they join. These rivers do not run directly into one another, but form, in the triangle just mentioned, a delta, composed of an intricate network of

channels, sloughs, and low islands. By extensive dredging and levee work much of this extremely fertile country has been reclaimed and brought into cultivation. The soil is a mixture of peat and
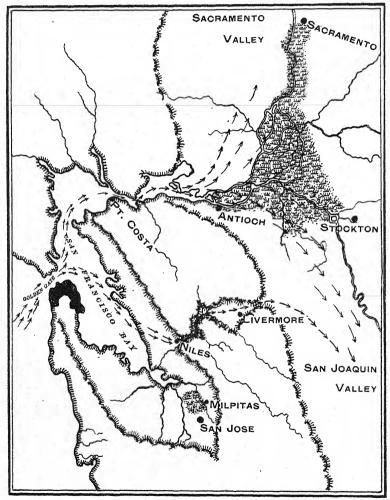


FIG. 3.—Map of central California, showing asparagus districts.

river sediment in various proportions, from almost pure formations of each to an equal mixture of the two. After reclamation and continued cultivation the level of these islands gradually sinks, and they become saucer-shaped, several feet below the river level outside

the levee (*fig. 5*). The soil is naturally full of moisture, but with levees, drainage, and rainless summers it may become extremely dry unless irrigated. Fires frequently occur in the peaty formation and cause serious damage. Irrigation is a simple matter in most cases, requiring only the placing of gates in the levee to admit and shut off the water.

While this country would at first seem to be one of excessive atmospheric moisture, the reverse is true in summer. Much of the reclaimed land becomes extremely dry, but most important is the position of this region directly at the opening of the great interior valley of California into San Francisco Bay and the Pacific Ocean (see *fig. 4*). Through this opening, formed by the Golden Gate at San Francisco and the Carquinez Straits at Port Costa, there blows in summer the strong, steady, so-called trade wind, coming in from the west, passing up through the straits, and then dividing north and south in response to the currents caused by the extreme summer heat of the great interior valley. In this asparagus country there occurs almost every day in summer a strong, dry, west wind which rises early in the morning and quickly dries what little dew may have been formed, except in sheltered spots. This wind, therefore, is an important and perhaps the chief factor in the amount of dew formation. Across the lower left corner of the triangle, where the wind is most constant, there is practically no dew in summer. Approaching the other two angles there is more, though much less than any eastern section.

At various points on the margin of San Francisco Bay are other asparagus districts, most important of which is that near Milpitas, comprising some 600 acres. This is situated, as may be seen, in a sort of pocket at the lower end of the bay, surrounded by high hills on both sides (*fig. 6*). The wind current coming in at the Golden Gate blows across the bay quite constantly and has a tendency to turn south toward Milpitas and the Santa Clara Valley below, but at Niles it is diverted into the interior valley through the Niles Cañon and Livermore Pass, which open through the hills at this point. Without lengthening this already extended description, it need only be said that this produces a condition at Milpitas much similar to that in the East as regards dew. Atmospheric moisture from the
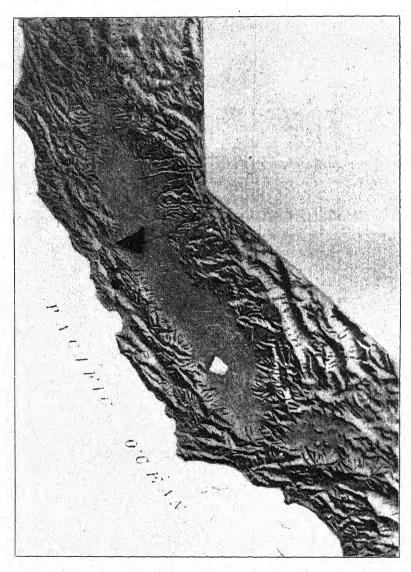
FIG. 4.—Relief map of California, showing the great interior valley and position of asparagus districts; Niles-Livermore Pass also indicated. Adapted from U. S. Department of Agriculture Yearbook, 1902.
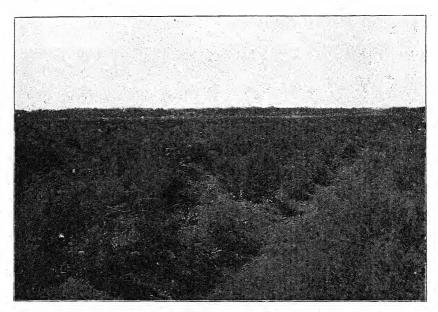
FIG. 5.—Typical island country, showing low level ground surrounded by levee.
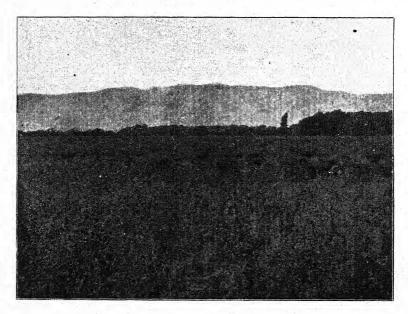


FIG. 6.—Typical asparagus field at Milpitas; high hills in distance.

nearby bay and ocean is abundant; heavy dews are frequent in summer and remain until late in the forenoon. The soil here is also more like the typical eastern asparagus soils, being of a light sandy nature, drying excessively in summer unless irrigated, which can be easily accomplished from artesian wells.

In both these districts the aecidial stage of the asparagus rust is extremely abundant in spring, following the winter rains, the condition shown in *fig. 2* being of ordinary occurrence in large areas. As the season progresses, this is followed at Milpitas with the usual development of the rust about as seen in the east; the aecidia are followed by an epidemic of uredo on the main cutting beds, which kills the tops quite generally and turns finally into black rust as a final stage. In the river country the progress of the disease is not so regular. As the season changes from moist spring to dry summer, the effect shown in *fig. 7* becomes evident. This is an aecidial patch upon a young stalk which started in the usual manner, but as the air became drier and dews less abundant its development was checked. Soil moisture was abundant, but it is seen from this not only that the fungus requires atmospheric moisture for its spore-germination, but that a certain degree is also needed for the development of spores from the aecidial patches. At this stage the mycelium is



FIG. 7.—Aecidial patch checked by lack of atmospheric moisture. Grand Island, Calif., July 13, 1903.



FIG. 8.—Aecidial patches drying out without developing spores; plant green and vigorous. Bouldin Island, July 28, 1903.

vigorous and ready for development, as may be proved by placing such a stalk in a moist chamber, when the "cluster-cups" break out in great luxuriance.   This is another direct water-relation of the rust, therefore, being apparently a provision for developing aecidiospores only when conditions are favorable for germination.   In the dry, windy districts such aecidial spots remain in this condition far into the
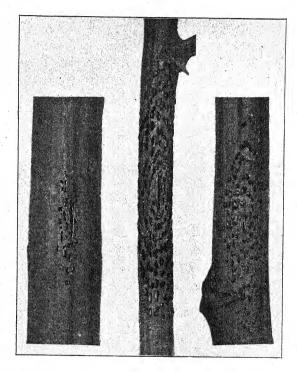


FIG. 9.—Uredo infection on green, vigorous stalks, checked and changed to teleuto by lack of atmospheric moisture.   Bouldin Island, July 28, 1903.

summer.   Finally, they pass into the state shown in *fig. 8*, the original aecidial areas drying out, leaving a feeble development of mixed uredospores and teleutospores about the edges.

Through the period of midsummer, from June to September, but little trace of rust can be found in most of this country.   Careful search, however, reveals here and there on volunteer growth in sheltered nooks the condition shown in *fig. 9*.   These are green

vigorous stalks, each with a single infection contracted earlier in the
season, which now appears as an almost pure teleutospore formation
directly on the green stalks. The value of these spores as reproduc-
tive bodies is doubtful, as they will not germinate at any time during
the summer. Apparently this is rather the form assumed by the
fungus under unfavorable conditions, when infection could not take
place, producing only the resting, teleuto stage. If such a stalk be
placed in a moist chamber, there immediately breaks out at the
outer edge of the infected area a circle of uredosori, with spores
capable of immediate germination. The same occurs in nature
later in the season as the dew becomes more abundant. Here again
is shown the same relation to atmospheric moisture in the case of
uredo development, proving that the fungus not only requires mois-
ture for the germination of its spores and for infection, but has the
same requirement for the production of spore forms capable of imme-
diate germination. Experiments by the writer show that both the
aecidiospores and uredospores of this fungus are comparatively
short-lived, but that the teleutospores are capable of lying dormant
for long periods and have a strong relation to the effect of frost in
their germination. This also shows the teleuto stage as not neces-
sarily a fall rust, but as occurring regularly under other conditions
extremely unfavorable to the further development of the fungus.

It is to be understood that these stages described are not indi-
vidual cases, but the regular development of the asparagus rust in
such a district as this. In September moisture becomes a little
more abundant, varying locally with the amount of irrigation and
other conditions, and now begins the regular uredo epidemic. This
starts invariably in the island country in corners and low places
sheltered on the west, such as are shown from actual experience in
*figs. 10, 11, 12, 13.* These are all of the same nature and represent
spots where uredo infection started two or three weeks before the
main beds in the open were affected. It is scarcely necessary to
say that such places will be avoided by growers in the future.

In the latter part of September the rust gradually works out into
the open fields. The trade wind is now subsiding, but blows fitfully
for days at a time. The disease still seeks shelter from this drying
influence and appears first on the east side of north and south rows,
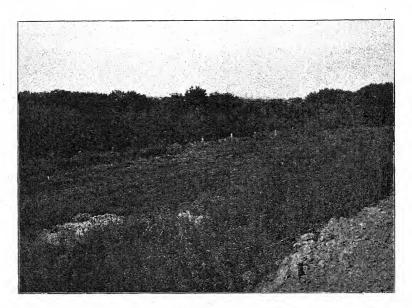
FIG. 10.—Corner of asparagus field sheltered from wind by willows and levee. Bouldin Island.
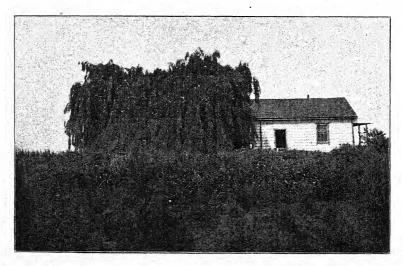


FIG. 11.—Bouldin Island schoolhouse, surrounded by asparagus fields and harboring rust on east side.

or in the sheltered places among the thick tops. Here it starts in
scattered spots, each very distinct, and if uninterrupted continues
spreading until late November, passing into the teleuto stage in the
ordinary manner. The feature shown in *figs. 14* and *15* is, however,
one of the most remarkable. In this particular instance the rust
started in the uredo form in the scattering manner just described.
*Fig. 14* is in a mass of tops sheltered by taller growth toward the west,
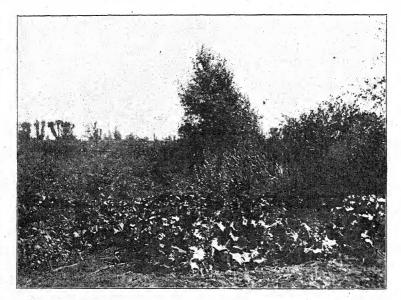


FIG. 12.—Old slough bed at Sacramento, with asparagus to left; starting point
of rust. August 14, 1903.

and *fig. 15* is the east end of an east-and-west row. Just as this was
well started (the condition all over the district was mostly the same),
the wind revived in a very dry form and blew steadily for a number
of days, with quite cold nights. Immediately the uredo rust on the
green stalks turned to teleuto, the rust stopped spreading, and the
fields looked exactly as though a fire-brand had been thrust into the
green tops here and there, producing a black, dead spot in the green,
healthy growth. The tops being still growing, new growth came
up through, and the fields were spotted with these perfectly black,
dead, teleuto-covered patches, surrounded by and in contact with

green healthy growth. *Fig. 16* shows a branch from the edge of the
dead spot with pure teleuto development on the green thrifty branches.
This condition lasted so long as the wind continued, then gradually
reverted to uredo infection, and the tops all became affected. This
shows more strikingly than anything else the effect of real atmos-



FIG. 13.—Asparagus at Sacramento, sheltered on west by trees; same effect as
in *figs. 11, 12, 13.*

pheric dryness upon *Puccinia Asparagi* at this stage of its develop-
ment, and the function of the teleuto form.

At Milpitas, where dew was quite abundant, though probably
scarcely as much so as in the east, and no summer rains occurred,
no such effects could be seen. Early in September everything was
badly rusted. Even here, however, one feature in connection with
the dew-relation is marked. This is the progress of the rust from
top to bottom of the stalks, seen in all cases of the disease in this
state. *Fig. 17* shows the condition well along in the season, the
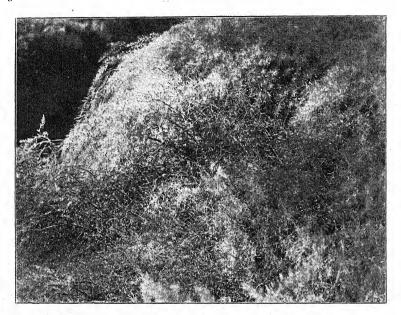
FIG. 14.—Dead, rusty spot in green asparagus tops where fungus was checked by wind and changed to teleuto form.   Bouldin Island, October 20, 1903.
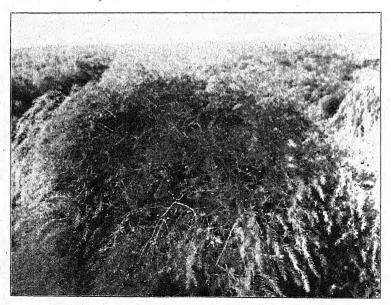


FIG. 15.—Same as *fig. 14.*

top shading and protecting the lower portion. *Fig. 18* shows the
bed still later, a condition which in beds well cultivated often lasts
until November. The writer has considered that this feature may
be due to the absence of rains to drive the spores more rapidly down



FIG. 16.—Teleutosori on green branches at margin of spots as in *figs. 14* and *15*.

through the tops, as he has never observed it in the east. By the
means shown in *fig. 19* the rust can be absolutely prevented in Cali-
fornia, although in Milpitas the covering must be thicker than on
the islands, where one thickness of light cheese-cloth is sufficient.

It may also be said here that from the writer's observations he has concluded that heavy rainfall has little to do in any section of the country with producing infection by the rust, since there is evidence to show that by this means the spores are actually washed from the smooth surface of the plant to a great degree, rather than being afforded opportunity for germination and infection. A copious, misty dew, remaining until late in the forenoon on the thick asparagus
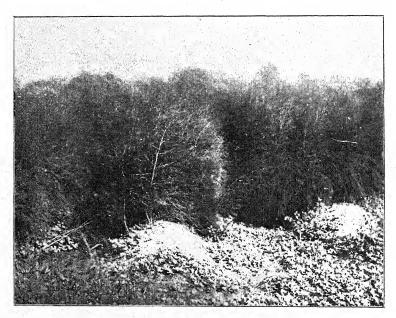


FIG. 17.—Effect of rust at Milpitas, working from above downwards. September 23, 1903.

tops, appears to be the most important factor in producing infection. Experiments with uredospores, placed out of doors on dry glass slides night after night in various situations, support this view, as well as extended field observations. During rain the spores are washed from the slides and carried away. This would not occur so entirely upon the plant, but is true to a very large extent. During nights of very light dew no germination occurred. With slight dew, drying away early in the day, germination started, but the germ-tubes dried up before they would have had time for infection. Most
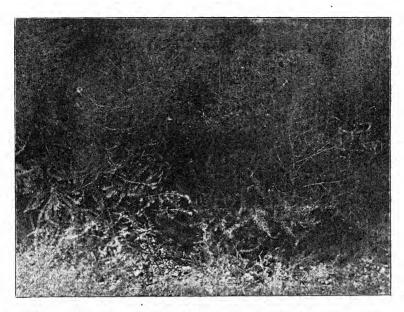
FIG. 18.—Condition late in the season of many California fields; green strip at bottom.   November 1, 1903.
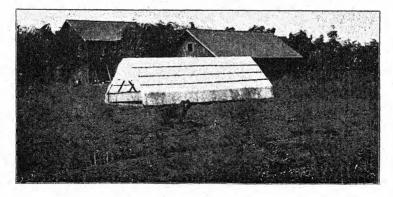


FIG. 19.—Tent over asparagus; tops just growing up.   Bouldin Island, July 14, 1903.

of these dews seem to form just before sunrise in California, so that they exist only a short time. On misty nights, with heavy dew, a most vigorous germination takes place, easily sufficient to produce infection. It has even seemed to the writer that germination in this way is more vigorous than in drops of distilled or tap water placed on the slide, though no exact comparisons have been made.

Something remains to be said as to the influence of soil moisture upon the rust in California. In the island district the wind effects are so absolute that all other features are of secondary importance. Soil moisture increases the amount of dew, and since almost all this country has abundant natural subirrigation, it is desirable to keep the surface as dry as possible. In the case of one plantation, particularly, situated in the strongest wind belt and where the nights were particularly dry, no rust whatever has developed, though in a center of infection, although the soil became so dry through neglect that cracks opened six inches wide and four feet in depth, and the asparagus roots were almost killed. It should be fully understood, however, that in this case there was absolutely no moisture in the air to germinate spores. A sheet of tissue paper lying on the ground would be as dry and crisp at sunrise as at noon. Such conditions are never approximated in the east.

At Milpitas, with considerable dew on all the beds, differences in soil moisture are more apparent. Some of the beds here are left unirrigated and uncultivated in summer and become extremely dry. In these the rust makes much more rapid headway than in the irrigated beds, and the tops are killed to the ground, while the others still have the green bottom (*figs. 17, 18*) late in the season. It is a general principle, in fact, that in this district, where conditions resemble those of the east, except for the absence of summer rain, the driest beds rust first and most completely, while those kept wet throughout the summer are the latest and least affected. This could not be shown more plainly than by the field in which *fig. 20* was taken. In this case a stream of water was being run past the end of a very dry asparagus field for irrigating lower down. When the whole field back to the right was dead with rust, the end plants in each row, next the water, were green and vigorous, as shown in the illustration. It is difficult to imagine how more absolute proof

could be found than this.  *Fig. 21* is along the same line, showing a low corner of a hundred-acre asparagus field, which portion remained green much after the tops in the drier portion of the field were dead. The water from irrigation accumulated here in the rusty season, with the effect described and illustrated.
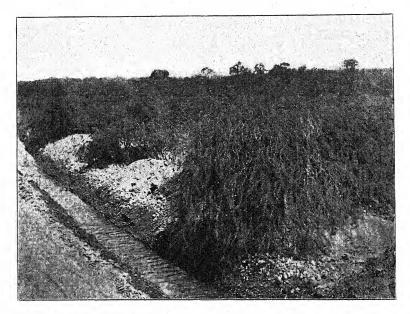


FIG. 20.—Effect of irrigation in region of dry soil and abundant dew.  Near San José, Calif., August 20, 1903.

The water-relation of *Puccinia Asparagi* may be thus summarized:

### DIRECT RELATION.

By direct relation is meant the effect of moisture (necessarily atmospheric, except possibly in connection with the germination of the teleutospores, which has not been touched upon) acting directly upon the spores or mycelium of the rust.  This relation has proved to be of foremost importance when absolute conditions prevail.  It has been attempted to show:

That dew is of absolute necessity in infection by the rust and of more importance than rain.

That without moisture of this sort no infection can take place, regardless of all other conditions.

That the effects of atmospheric dryness are not limited to the spore-germination, but produce the following effects upon spore production in cases of previous infection: Aecidial development is checked, no "cluster cups" appear, and the mycelium remains dormant for some time; if moisture conditions occur, spores are at once
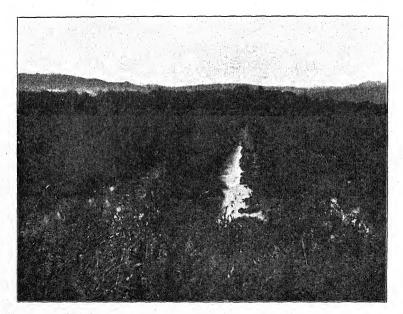


FIG. 21.—Showing same as *fig. 20*.  Milpitas, August 20, 1903.

produced, otherwise the mycelium finally dies out.  Uredo development is similarly checked and changes to a production of teleutospores in the sori already formed, without regard to season or condition of the host; with moisture uredospore formation begins again at once.

That the teleuto stage is a provision for surviving any condition unfavorable to the fungus, whether of food supply, moisture, temperature, or resistance by the host, without regard to season.

That extremes of atmospheric moisture conditions are insufficient in most sections of the country to bring out or make effective this direct relation.

### INDIRECT RELATION.

By this is meant the effect of moisture acting upon the parasite through its effect upon the host, and limited therefore to soil moisture. It has been attempted to show in this respect:

That under any but very unusual conditions of atmospheric moisture the indirect relation is of greatest importance.

That an abundance of soil moisture during the summer has a marked effect in retarding the development of this fungus by giving the host greater vitality and resistance.

That this is shown by the effects of the varying summer rainfall in different seasons, by the differences in the water-retaining capacity of different soils, and by the effects of irrigation.

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# DELTA AND DESERT VEGETATION.

### Daniel Trembly MacDougal.

### (WITH SEVEN FIGURES)

THE systematized discussion of the deserts of North America recently attempted by Mr. Coville and the author[1] made it obvious that the southern extension of the Nevadan-Sonoran desert in Sonora and peninsular California around the head of the Gulf was practically a *terra incognita* to the naturalist.

The waters of the Gulf have been surveyed and the more prominent features of the shore lines traced, but since this work was done thirty years ago, the charts, originally made from data collected by "Commander" George Dewey in 1873–75, are sadly in need of revision, especially in the region contiguous to the mouth of the Rio Colorado. The positions of the prominent hills and mountains visible from the sea have been plotted as range marks for the navigator, but the maps bearing the results are difficult of interpretation by the explorer on land.

A fair share of attention has been paid to the animal life of the river and Gulf, but the extensive areas around the mouth of the river and the head of the Gulf have so far practically escaped investigation. These regions offer difficult problems of transportation and subsistence to the explorer. The southern part of the delta includes vast areas of muddy salt flats cut by a labyrinth of shallow pools and channels, and joining directly the desert slopes and plains of Baja California and Sonora. The water in the lower course of the river is brackish for a distance of $30^{km}$ from the sea, while other sources of water are uncertain and widely separated, the tropical sun forming an additional factor to test the endurance of the unaccustomed traveler. In running the boundary on the long northwestward slant of the Arizona-Sonoran line after the Gadsden Purchase Treaty, the commission found it necessary to haul water nearly $200^{km}$ to meet the needs of its camps. The trail which runs near the bound-

[1] COVILLE, F. V. and MacDOUGAL, D. T., The Desert Botanical Laboratory of the Carnegie Institution. November, 1903. Washington, D. C.

ary across a typical portion of the desert mesa was the route followed by Mexican prospectors rushing to the Californian gold fields in 1849, and in the waterless stretch of 150$^{km}$ between Quitovaquito and Tinajas Altas may be counted over four hundred small circles and crosses of loose stones by the side of the trail, grim evidences of failures to negotiate this formidable "Jornada del Muerto."

Attempts to penetrate the desert directly from the coast have met with equally serious difficulties. The shore is fringed with mud flats many kilometers in width, and numerous sand bars bare at low water; the tides rise 4–10$^m$ and produce currents that run 4–8$^{km}$ per hour, forming waves or bores that sweep up the river, at times endangering all craft not in protected anchorages. But few sheltered anchorages are to be found in the upper Gulf, and nearly all of these are far from a supply of fresh water. The few expeditions to this region in which attention was paid to the flora are easily recounted.

Colonel Andrew B. Gray traversed the desert from the international boundary to Adair Bay in 1854, discovering the singular parasitic *Ammobroma Sonorae* Torr.,[2] which fastens to the roots of Franseria and Dalea at depths of 60–120$^{cm}$ in the sand, and sends its fleshy stems to the surface, on which the flowers appear to rest.

Dr. E. Palmer traveled southward from Yuma to Lerdo near the head of tidewater in 1889, and collected about two dozen species of plants,[3] but no general account of the expedition is available.

Descriptions of a number of the plants are to be found in the accounts of the boundary survey,[4] in which but little attention, however, appears to have been paid to the flora of the delta.

T. S. Brandegee[5] made a long journey overland, in the same year in which he traversed Baja California, for a distance of several hundred miles northward to San Quintin in about the same latitude as the southernmost point reached by my own expedition. However, he did not reach the country east of the main divide north of San Luis Bay, 300$^{km}$ south of the mouth of the river.

[2] TORREY, J., Ammobroma, a new genus of plants. Ann. Lyc. Nat. Hist. N. Y. **8**: June 1864.

[3] ROSE, J. N., Contrib. U. S. Nat. Herb. **1**:27. 1890.

[4] Report on U. S. and Mex. Boundary Survey, Emory **2**:21. 1859.

[5] BRANDEGEE, T. S., A collection of plants from Baja California, 1889. Proc. Calif. Acad. II. **2**:—. 1889.

Mr. Edmund Heller made some explorations and zoological collections for the Field Columbian Museum, February–December 1902, in which the western slopes of the Santa Catalina, San Pedro Martir, or Calamuie Mountains and of the Hanson Laguna Mountains were traversed.    Mr. Heller crossed the main divide in about latitude 31° 30′, south of the main elevation of Calamahuie, to Parral, which lies about 600$^m$ above sea level.    One degree to the northward the main range was again crossed at San Matias Pass and his expedition reached the bay of San Felipe.    The account of this work contains notes on the occurrence of many important plants, including the giant cactus and the Washington palm.[6]

The author organized an expedition to this region early in the present year, under the joint auspices of the Desert Botanical Laboratory of the Carnegie Institution, and of the New York Botanical Garden.    In accordance with plans made a year previously, Mr. G. Sykes, civil engineer, of Flagstaff, Arizona, proceeded to Yuma in November 1903, where the construction of a small sloop, 9$^m$ in length with 2.4$^m$ beam, was begun and which was brought to completion late in January 1904.    This boat was of a flat-bottomed design suitable for floating down the muddy shallows of the river, and was furnished with a centerboard for use in sailing the rougher waters of the Gulf, being rigged with a mainsail and jib.

In addition to the camp equipment, which included means for storing and carrying fresh water, and a special form of portable canteen, provisions, compasses, binoculars, cameras, aneroids, thermometers, hygrometers, and other material to a total weight of about 500$^{kg}$ was taken aboard.    The party included Prof. R. H. Forbes, Director of the Agricultural Experiment Stations of Arizona, and an assistant, in addition to Mr. Sykes and the author.    A general narrative in which the detailed movements of the expedition are given has already been published[7] and need not receive further attention in this article.

[6] ELLIOT, D. G., A list of mammals collected by Edmund Heller in the San Pedro Martir and Hanson Laguna Mountains and the accompanying coast regions of Lower California.    Field Columbian Museum, Publ. 79.    Zoological Series **3**: no. 12. 1903.

[7] MACDOUGAL, D. T., Botanical explorations in the southwest.    Jour. N. Y. Bot. Garden **5**:89. 1904.

## THE DELTA.

The expedition cast loose from the shore at Yuma at noon on January 28, and within a short distance below the sand bluffs on either hand curved away from the stream, and we were fairly in the great delta which extends from this point to the Gulf of California, a distance of about $140^{km}$; while the coastal plains on the western side of the Gulf embrace mud flats that constitute an actual extension of the delta $50^{km}$ further. This delta probably offers more varied and striking features of natural history than any other watercourse in North America. The river which has formed it rises in the perpetual snows of Utah, Wyoming, and Colorado, and runs $2500^{km}$, chiefly through arid regions, before it empties into the upper end of the sub-tropical Gulf, into which it carries sixty million tons of sediment yearly, building up the delta and extending it seaward at a rate visible to common observation within a single lifetime.[8] Numerous witnesses among the Cocopa Indians, Mexicans, and river men are agreed that the various distinct associations of plants characterized by salt grass, willow, and poplar, have advanced about $12–14^{km}$ to the southward during the last fifty years.

The portion of the delta near the present course of the river consists of an alluvial plain, not more than $4^m$ above the low-water mark, subject to constant bank erosion, shifting, and remaking of the soil, cut in all directions by old channels existing as bayous and sloughs, and flooded at high water in May, June, and July. Almost pure formations of willow and poplar (*Populus mexicana*) cover many square kilometers and furnish food for thousands of beavers that burrow in the banks. The poplar is thickly infested with a mistletoe (Phoradendron), and fungal parasites are abundant. Large areas are occupied by the arrow-weed (*Pluchea sericea*), and mesquite (*Prosopis velutinea*), and the screw-bean or "tornilla" (*P. pubescens*). Two or three species of Atriplex are also to be found in sections in which the action of the water prevents the establishment of the woody perennials of greater size. In the upper part of the delta a cane (Phragmites) fringes the channel, and its closely interwoven roots act materially in preventing erosion of the banks.

[8] FORBES, R. H., The Colorado river of the west. Univ. of Ariz. Monthly **6**:112. 1904.

In the lower part of the delta, where the river is affected by the spring tides, the cane is partly replaced by a cat-tail "tule" (*Typha angusti-folia*), which not only lines the shores for many miles, but extends back some distance on areas free from trees, forming dense masses
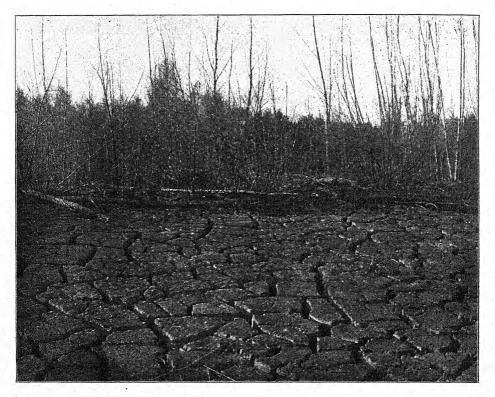


FIG. 1.—Scene on right bank of Rio Colorado, Baja California, a few meters from the margin of the stream, 10$^{km}$ below Yuma; the conchoidal fractures of the clayey mud are 30–35$^{cm}$ in depth; Salix and Populus in background; Station 1 of hygrometric observations.

that afford shelter for a number of animals, including a peculiar sub-species of a small mountain lion.

Large areas throughout the delta which were not covered by trees bore wild hemp (Cassia?) in great abundance. The slender stems reach a height of 3–4$^{m}$, branch profusely above, and bear numerous pods. At the time of our visit, the plants which were annuals were

dead and dry, still retaining the seed pods, and progress through one of these plantations was accompanied by a shower of seeds which results from any disturbance of the plant. The clearings also furnished suitable conditions for a plant with a deeply buried bulb, probably a Calochortus, which is eaten by the Cocopa Indians under the name of "chech," and also forms an important article of food of the sand-hill crane, and of the wild hogs that infest the tules.

The forests of willow and poplar begin to lose density at a distance of 50–60$^{km}$ from the Gulf, the willows extending farthest toward salt water, a few being seen near the mouth of the Hardy branch of the Colorado. Beyond these are the mud plains, the portions not actually subject to erosion being thickly covered with salt grass (*Distichlis spicata*) and *Cressa truxillensis*, and bearing small clumps and isolated specimens of salt bush (Atriplex), mesquite, and screw bean. Such areas are inundated at the highest tides; consequently the soil solutions are heavily charged with salts, and whitish alkaline crusts appear during the winter dry season.

The floods of spring and early summer from the rains and melting snows of the headwaters region of the river raise the level of the water until it flushes the innumerable old channels and covers the greater part of the delta. Most of the herbaceous species make their annual growth after the waters have subsided in July. Other species, which are less affected by the lower temperatures and low relative humidity of the winter season, are set in action by the favorable conditions of March and April, and come into bloom at this time, thus making two distinct seasonal groups of annuals.

The main stream of the river cuts directly into the gravel plain or mesa of Sonora at four points on the eastern margin of the delta, and here are to be seen the striking contrasts of the isolated xerophilous plants of the dry gravelly soil of the desert within a few meters of the pure dense formations of the muddy soil of the alluvial plain of the delta (*fig. 2*). In places the creosote bush (Covillea) descends the gentler slopes to the margin of the moister soil near the margin of the channel, accomplishing a growth which carries it to a height of over 7$^{m}$, the maximum size for the species.

The above description applies most directly to the eastern and southern portions of the delta, which may be observed in the descent

of the river, but it by no means exhausts the interesting features of the region. If the low-lying contiguous areas to the westward capable of being flooded are included, the delta may be said to have an area approximately equal to the state of Connecticut. One arm extends over $200^{km}$ to the northwestward and includes the Salton Basin, with its exposed bottom more than $130^m$ below the level of the sea. Although the summer floods of extreme height find their
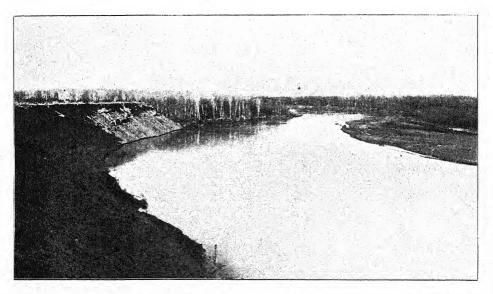


FIG. 2.—View of Rio Colorado at a point where it cuts into the desert mesa of Sonora a few kilometers south of international boundary; looking downstream; Populus and Salix on right bank; dense forest of Populus in background on left bank; portion of mesa in foreground on left bank with Covillea, Stillingia, and Ephedra; Station 3.

way by old channels into this basin, creating a temporary lake of great extent, yet the district affected must be classed as desert, since the highly saline character of the soil and prevailing low humidity and precipitation support representative types of vegetation (*fig. 4*).[9] Other basins ordinarily dry, with saline deposits, are to be found in various parts of the depressed area, which has the characteristics of a sea-floor of comparatively recent date.

[9] See also COVILLE and MACDOUGAL, The Desert Botanical Laboratory of the Carnegie Institution (November 1903), pp. 21–22. *pls. 23–26.*

Many parts of the delta and of the adjoining districts in the deserts of Sonora and Baja California show traces of recent earthquakes and of volcanic action, a tract 2 by 10$^{km}$ being now occupied by a number of active mud volcanoes.
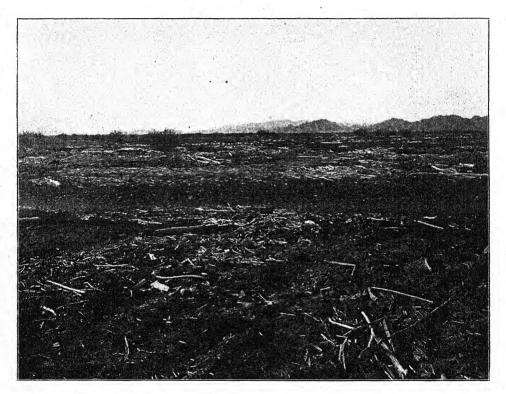


FIG. 3.—View to southward on floodplain of Rio Colorado below mouth of Hardy's branch; Range Hill in distance; carpet of *Cressa truxillensis* and *Distichlis spicata;* Prosopis scattered over plain, which also shows great quantities of driftwood.

The Cocopa Mountains rise directly from the delta to a height of over 1300$^m$, and their granite slopes support an island of desert vegetation of the types induced by low humidity and precipitation.

## DESERTS.

The arid region east of the delta, extending southward from the Gila River, consists principally of long gentle slopes or sandy gravelly plains rising gradually toward the interior, and broken here and there

by a succession of low mountain ranges, such as the Agua Dulce, Pinacate, and Santa Clara Mountains. The soil is particularly subject to the action of the wind, but the irregular consistency of the sand allows the formation of moving dunes or "sables" in a few localities only near the delta. Mounds of a few meters in height, held together by the roots of Ephedra, Covillea, and other shrubs, are numerous, however, such mounds being due either to the erosion of the soil around them, or to its accumulation and retention by the
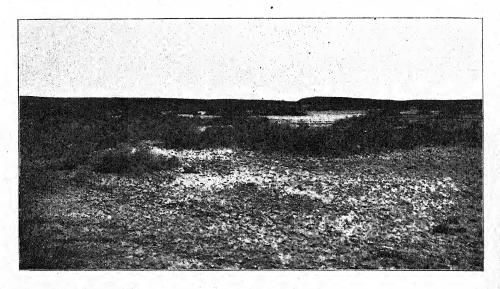


FIG. 4.—View in Salton Basin, California; the surface of the soil is thickly incrusted with saline matter in the open spaces; the vegetation consists chiefly of Spirostachys and Atriplex.

clumps of plants. In addition to the few herbaceous annuals which arise during the season favorable for growth, the principal types are perennials with spinose branches and reduced deciduous leaves, although a few species with hardy leaves are included. *Ephedra, Gaertneria albicaulis, Oenothera claviformis, Lupinus mexicana, Abronia villosa, Astragalus Vaseyi, Plantago scariosa, Langloisia Schottii, Stillingia annua, Asclepias subulata,* and *Fouquieria splendens* are typical examples; while a few forms with deeply lying bulbs are also found here, including *Hesperocallis montana (fig. 5).*

The character of the portion of the Colorado desert lying within the state of California is the subject of a recent paper by S. B. Parish,[10] and need not be discussed further here. He says, concerning the delta: "the region bordering the Colorado River is too little known to permit exact statements regarding it."

The arid region of Baja California to the eastward of the main divide covers an area of much greater topographical diversity, but
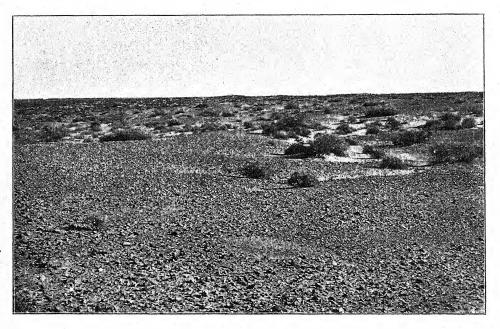


FIG. 5.—View to southeastward from Lerdo, Sonora; the gravel mesa bears scattering bushes of Covillea and Ephedra.

with less rainfall probably than the Sonoran slopes across the Gulf, from which its flora is widely different in general composition. My examination of this part of the country was made from San Felipe Bay, which lies about 60$^{km}$ south of the mouth of the Rio Colorado in latitude 31° N. The western shore of the Gulf between this point and the river is made up of a continuation of the mud-flats of the delta, and has great expanses covered with Cressa and salt grass.

[10] PARISH, S. B., A sketch of the flora of Southern California. BOT. GAZ. **36**:203–222, 259–279. 1903.

The central elevation consists of the mountain ridge which culminates in the peak of Calamahuie at an elevation estimated at about 3300$^m$. To the eastward it breaks into lofty precipices and steep slopes which have not been surmounted between 30° 30′ and 32° 30′ N., no passes having been found in this wild stretch of 100$^{km}$. Between the main range and the coast lie numerous minor ranges disposed in labyrinthine complexity, which also have not been explored. So far as available information may be relied upon, no botanist had previously visited this region, and some care was taken to secure living and preserved specimens of the native plants whenever at all possible.

The lower coastal slopes were found to be sandy and gravelly, the depressions and near the shore furnishing suitable conditions for *Lycium Torreyi* and *Parosela spinosa*, which latter· becomes a tree 7$^m$ in height. *Asclepias subulata* was abundant in clumps, and *Ditaxis serrata* grew on level areas. Other species, characteristic of the lower levels, were *Ibervillea tonella*, *Croton californicum*, *Lupinus mexicanus*, and the curious *Frankenia Palmeri*. The low alkaline pockets reached by the spring tides furnished conditions suitable for *Spirostachys occidentalis*. Covillea, with its enormous capacity of adjustment, extended from near the shore across the entire slope and up the granite mountains through a range of over 600$^m$ in elevation. The various portions of the slope between the sea and the first range of mountains supported ocotillo (*Fouquieria splendens*), which attained its maximum height of 10$^m$, palo verde (*Parkinsonia microphylla*), palo fierro (*Olneya tesota*), Bursera, and *Gaertneria icilifolia*. The streamways leading down from the mountains were inhabited by a number of Eriogonums and euphorbiaceous herbs. A few Opuntias of the cylindrical arboreous type, an Echinocactus, a Mammillaria, and a small Cereus were also seen. *Pilocereus Schottii*, which is found on the mainland far southward, here reaches the greatest density yet observed, forming dense forests, acres in extent. Perhaps the most notable feature from a geographical point of view was shown by the presence of a great tree cactus, having the appearance of *Cereus pecten-aboriginis*. *Cereus Pringlei* is known to be abundant under the common name of "cardon" farther south, but this plant appears to agree with the former, and makes a splendid picture in the arid landscape, finding here its extreme northern limit of known occurrence.

The large number of species with laticiferous juices was especially noticeable, but with the exception of the dozen Cacti no plants with organs for the storage of water were seen, a fact possibly connected with the extremely low precipitation and low water content of the soil at all times. Seeds of a Cenchrus were very abundant and were
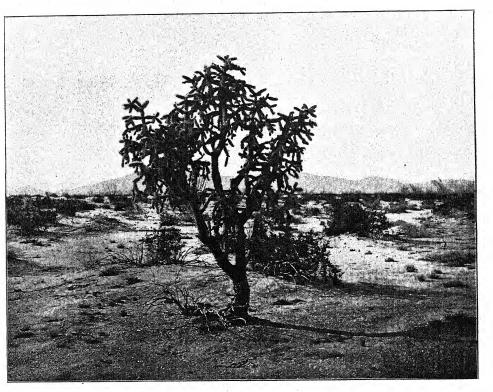


FIG. 6.—Desert of Baja California, looking westward from beach north of San Felipe Bay; Opuntia, Covillea, and Fouquiera.

used by burrowing rodents as a means of fortification of the entrances to their burrows, in the same manner that the joints of the "cholla" are employed elsewhere.

A mountain to the southwestward of San Felipe Bay was climbed and a summit reached at an elevation of over 1000$^m$. The granite slopes supported a sparse vegetation of such types as Mammillaria, Ephedra, *Bursera microphylla, Asclepias albicans, Eriogonum infla-*

*tum,* Yucca, Agave, and Opuntia. So far as might be estimated by the instruments at hand, the mountain is probably the one on the hydrographic map of 1873–75 designated as a "sharp white peak 4288[ft]," which had not previously been ascended, and still bears no name.

### METEOROLOGICAL FEATURES.

Data bearing on the climatic conditions in the delta and of the contiguous deserts are very meager. Records have been kept at Yuma for a long term of years, and some data obtained at Torres, Sonora, quoted in the recent contribution by Mr. Coville and the author,[11] constitute the only information available. The following table taken from the records of the U. S. Weather Bureau[12] gives the conditions at the head of the delta.

The transcript of the record was furnished by Hon. Willis L. Moore Chief U. S. Weather Bureau.

| 1903 | Jan. | Feb. | March | Ap·il | May | June | July | August | Sept. | Oct. | Nov. | Dec. | Total | Normal |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Maximum temperature | 76 | 82 | 90 | 97 | 106 | 112 | 111 | 113 | 112 | 96 | 87 | 80 | .. | .. |
| Minimum temperature | 33 | 29 | 38 | 47 | 50 | 60 | 69 | 72 | 59 | 51 | 42 | 34 | .. | .. |
| Precipitation | .. | .23 | .. | .. | .. | .. | .04 | .. | .67 | .04 | .. | .. | .98 | 2.98 |
| Average precipitation (1876–90) | .39 | .45 | .18 | .12 | .06 | .. | .13 | .40 | .13 | .21 | .35 | .64 | 3.06 | .. |

### MEAN RELATIVE HUMIDITY.

#### 8 A. M.

| Year | Jan. | Feb. | Mar. | April | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1903 | 53.5 | 62.9 | 53.3 | 52.0 | 61.3 | 59.9 | 61.1 | 68.3 | 67.4 | 54.3 | 46.7 | 39.5 |
| 1904 | 43.0 | 45.7 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |

#### 8 P. M.

| Year | Jan. | Feb. | Mar. | April | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1903 | 28.0 | 44.8 | 23.0 | 17.0 | 17.9 | 17.8 | 21.7 | 2.82 | 30.9 | 23.7 | 28.4 | 24.2 |
| 1904 | 20.7 | 21.7 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |

It is to be seen that the delta and the contiguous districts have an annual precipitation of less than 7[cm], and that less than 2[cm] was

[11] Desert Botanical Laboratory of the Carnegie Institution, p. 23. November 1903.

[12] GREELY and GLASFORD, Report on the climate of Arizona. Ex. Doc. No. 287. Washington. 1891. Climate and Crop service, U. S. Weather Bureau. Report for Arizona Section for 1903.

received during the year 1903, the relative humidity at all times being very low also. The rainfall is distributed throughout the year, so that only a small proportion of the total is received within any month; furthermore, this distribution is irregular in any series of seasons, so that the native plants have but little opportunity of acquiring a
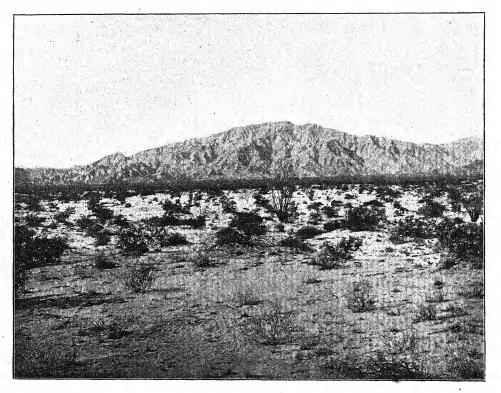


FIG. 7.—Desert of Baja California; view from San Felipe Bay; peak over 1000ᵐ high, ascended February 14, 1904, in distance; the sloping plain which rises gradually to the foot of the mountain bears Fouquieria, Ephedra, Covillea, Bursera, Parosela, Parkinsonia, and Cereus.

rhythm of activity in response to the annual supply of moisture, a fact not without its influence on the general anatomical character of the plants, as will be pointed out below. In no part of the country to the southward of Yuma did we find any evidences of a greater rainfall than that given above, upon noting the surface of the soil

and the state of resting vegetation, and no precipitation occurred during the month the expedition was actually in field. Attention is to be called to the table of relative humidity, in which it is to be seen that the minima are very low, yielding averages from 17 to 30 per cent. So far as a general inspection could be relied upon, it did not appear that precipitation had occurred at San Felipe Bay within three months, and it might well have been three times that period since any had been received.

Dr. Edward Palmer visited the Raza Islands in the lower part of the Gulf, 225$^{km}$ northwest from Guaymas, in February 1890, and notes that no rainfall had been received there for more than a year.[13] Nothing can be hazarded as to the extent of the region with this extreme limit of aridity on the Sonoran side of the Gulf, except that it does not include the mesa at an elevation of 300$^{m}$ at Torres, and it does not appear to include the western slope of the central range in Baja California, although no definite information is available. So far as known at the present time, therefore, this region of extreme and constant drought, constituting the most pronounced type of desert in North America, lies on the eastward or lee side of the San Pedro Martir range of Baja California, and includes areas on the Sonoran mainland, the whole being a southern extension of the Colorado desert. It is evident, however, that a further investigation of the region is necessary to determine the exact meteorological status of this area, as well as the general character, derivation and relationships of its flora. The extreme type of strict desert offered by the area in question points to the possibility of finding here the readiest solution of some of the more important problems presented by desert vegetation.

### RELATIVE HUMIDITY IN DELTA AND DESERT.

The relatively brief time during which the expedition was in the field made it impossible to secure records of value as to precipitation, although it has been noted above that no rainfall occurred, except perhaps on the higher peaks of the Cocopa Mountains and of the main range in Baja California. A Lamprecht's hair hygrometer was carried, however, and observations were taken daily, the instru-

[13] Contrib. U. S. Nat. Herb. **1**: 79. 1890.

ment being compared before being taken into the field and after its return with other instruments for standardization. The data given below are corrected results, not direct transcripts from the notebook.

### Station 1.

Camp on dried mud flats on shore of Rio Colorado a kilometer below international boundary in Baja California; observations taken twenty feet from margin of bank amid willows and poplars; wind blowing offshore; see *fig. 1*.

| Jan. 28 | 4:30 P. M. | 60° F. | 17% rel. hum. |
| " 28 | 6:30 " | 55 " | 15 " |
| " 28 | 8:00 " | 51 " | 18 " |
| " 29 | 12:45 A. M. | 32 " | 41 " |
| " 29 | 1:20 " | 30 " | 50 " |
| " 29 | 6:00 " | 29 " | 66 " |
| " 29 | 6:25 " | 27 " | 70 " |
| " 29 | 7:00 " | 38 " | 60 " |
| " 29 | 7:40 | Sun on instrument | 36 " |

### Station 2.

Camp on small island in great bend 33$^{km}$ downstream from Yuma, covered with a dense grove of Salix except at one end.

| Jan. 29 | 4:50 P.M. | 61° F. | 21% rel. hum. |
| " 29 | 7:10 " | 37 " | 75 " |
| " 29 | 8:45 " | 32 " | 57 " |
| " 30 | 2:45 A. M. | 30 " | 84 " |
| " 30 | 5:45 " | 26 " | 58 " |
| " 30 | 7:50 | Sun on instrument | 35 " |

### Station 3.

Camp at lower end of high mesa bank below La Grulla, Sonora; observations taken at a point 60$^m$ from margin of bank 13$^m$ in height, constituting bank of river, among bushes of Covillea, Ephedra, etc. (*fig. 2*).

| Jan. 30 | 4:40 P. M. | 70° F. | 19% rel hum. |
| " 30 | 4:50 " | 68 " | 16 " |
| " 30 | 7:00 " | 54 " | 15 " |
| " 30 | 8:30 " | 48 " | 27 " |
| " 31 | 6:30 A. M. | 44 " | 30 " |
| " 31 | 7:30 " | 45 " | 29 " |

### Station 4.

Noon stop made at point where the river cuts into the Sonora mesa above "Noche Buena" cut-off; observations made at a point corresponding to Station 3, with similar vegetation.

Jan. 31  1:45 P. M.  72° F.  15% rel. hum.

### Station 5.

Camp on dry shore in Baja California among willows, poplar, and saltbush, with numerous beaver slides along bank.

| Feb. | 1 | 7:00 P. M. | 50° F. | 30% rel hum. |
| " | 1 | 8:30 " | 44 " | 66 " |
| " | 2 | 6:30 A. M. | 41 " | 59 " |

### Station 6.

Group of adobe buildings at Colonia Lerdo, on margin of gravel mesa sloping gradually to the delta, $2^{km}$ from stream, among mesquite, saltbush, and arrow-weed.

| Feb. | 3 | 11:40 A. M. | 78° F. | 16% rel hum. |
| " | 3 | 1:30 P. M. | 81 " | 11 " |
| " | 3 | 4:15 " | 79 " | 10.5 " |

### Station 7.

Camp on eastern shore of river at Colonia Lerdo, among poplar, willow, cane, and tule, $25^m$ from margin of water and $2^m$ above surface.

| Feb. | 5 | 7:25 P. M. | 64° F. | 38% rel. hum. |
| " | 5 | 7:45 " | 64 " | 40 " |
| " | 5 | 2:10 " | 67 " | 37 " |

### Station 8.

The data given below were obtained at a number of points on the plain and mountains, near camp on San Felipe Bay, Baja California.

#### Tent on beach.

| Feb. | 11 | 6:20 P. M. | 52° F. | 42% rel. hum. |
| " | 11 | 8:20 " | 49 " | 39 " |
| " | 12 | 5:50 A. M. | 37 " | 44 " |
| " | 12 | 8:00 " | 56 " | 27 " |
| " | 12 | 8:35 " | 63 " | 24 " |

In shade of Bursera.

At 76$^m$ level, 13$^{km}$ from shore.

| | | | |
|---|---|---|---|
| Feb. 13 | 1:00 P. M. | 71° F. | 40% rel. hum. |
| " 13 | 6:15 " | 57 " | 41 " |
| " 14 | 6:00 A. M. | 60 " | 33 " |

800$^m$ on mountain.

| | | | |
|---|---|---|---|
| Feb. 14 | 8:45 A. M. | 69° F. | 32% rel. hum. |

1200$^m$ on mountain (*fig. 7*).

| | | | |
|---|---|---|---|
| Feb. 14 | 11:00 A. M. | 72° F. | 32% rel. hum. |

Small mountain 100$^m$ high, 20$^{km}$ north.

San Felipe, 8$^{km}$ from coast.

| | | | |
|---|---|---|---|
| Feb. 19 | 9:45 A. M. | 72° F. | 18% rel. hum. |

## RÉSUMÉ.

It is to be seen that the region discussed in the foregoing paper includes a subtropical delta of irregular outline and long extensions, which includes within its outermost boundaries a great alluvial plain subject to floods, bank erosion, and shifting of the soil, and also to the action of salt tidal waters; a mountain range of granite and volcanic rocks over 1000$^m$ in height; a small area of active mud volcanoes; a depressed region, presumably an old sea-floor, the bottom of which is more than 100$^m$ below the level of the sea; and the mud flats near the actual mouth of the river. This delta is directly in contact with the gravel and sand desert mesas of Sonora and Baja California.

The portion of the delta subject to the direct action of the floods and tides is everywhere slightly alkaline and varies but little in the general constituency of the soil, supporting a luxuriant growth of vegetation, the more important elements of which grow in pure formations of the greatest possible density. The larger woody plants of this region have their bases submerged in water at a low temperature during the summer season, during which time the crowns are exposed to low relative humidity at temperatures that may be as much as 70° F. higher than the roots. In consequence of this condition many species in the low lands have xerophilous foliage. In addition, a comparatively high concentration of soil salts must be endured during the stages of low water.

An analysis of the flora of the region shows that many of the species of the delta extend down along the coast especially in the

regions with fringing mud banks derived from the river deposits. The greater part of the vegetation of the coastal slopes and plains, however, is made up of species which also extend southward along the shores of the Gulf, and are found but sparingly to the northward.

The vegetation of the Salton basin is subjected to the action of extreme aridity and also of a high concentration of soil salts, comprising types of the most pronounced character, both of halophytes and xerophytes. The elevations included in the delta are dry mountain slopes and support a desert vegetation.

The mesas adjoining the northern part of the Gulf of California appear to offer the most extreme desert conditions in North America. The rainfall at Yuma at the northern extremity of the delta was less than $25^{mm}$ during 1903, and years have been noted at points farther south in which no precipitation occurred. The entire normal precipitation in the desert in Baja California is probably no greater than the amount of water condensed as dew in eastern United States. The desert apparently extends to the slopes of the central elevation of the peninsula to the westward, which reaches an elevation of over $3000^m$. This mountain wall probably acts as a barrier which shuts off moisture-laden winds from the Pacific and causes the aridity of the region. The southern and eastern limits of the extreme desert cannot be defined with the information now at hand.

The vegetation of the desert areas in the regions of greatest aridity consists chiefly of types devoid of massive storage organs, and of perennials with laticiferous sap, while a large number of forms secrete volatile oils or exude resinous gums. The determination of the causal relations of these adaptations cannot be made safely by a general interpretation of the aspects of vegetation, but it is to be seen that in a region in which surplus rainfall or ground water never occurs, storage organs would be manifestly useless, and indeed their formation impossible. Species with spinose branches and minute leaves which are quickly discarded during unfavorable periods are abundant. Several species of Ephedra with functionally useless leaves and chlorophyllose stems are included, while Lycium and Frankenia with small succulent easily detachable leaves are highly characteristic of some localities; the last-named species are about

the only species offering anything of the nature of water-storage organs outside of the Cacti.[14]

The region under discussion offers matchless opportunities for comparison of the most highly developed xerophytic types of the desert with the broad-leaved forms of the delta which root in the mud. Midway between the two are the species which stand in the moist soil of the delta, and have foliage suitable to endure the extreme aridity of the air, which constantly blows from the desert over the entire delta.

NEW YORK BOTANICAL GARDEN.

[14] MACDOUGAL, D. T., Some aspects of desert vegetation. Plant World **6**:249–257. 1903.

# BRIEFER ARTICLES.

## THE AECIDIUM OF MAIZE RUST.

THE great economic importance of the corn (maize) crop lends special interest to any discovery relating to the habits and development of corn parasites. It is partly for this reason, and partly because it illustrates a method of observation not yet commonly understood, that the following narrative of the discovery of the aecidium of *Puccinia Sorghi* Schw., the common rust of corn, is given here in advance of the season's culture work, of which it forms a part, and which has been undertaken in cooperation with the Bureau of Plant Industry of the U. S. Department of Agriculture.

As corn rust is practically coextensive in geographical distribution with the cultivation of its host, although rarely so abundant and destructive as to attract the attention of the cultivator, and as no aecidium has seemed even in the remotest way to have connection with it, the view has gained ground that either an aecidium is no longer produced in its life-cycle, or that it occurs only in regions where corn was originally wild. In the latter case the aecidium might inhabit some host of restricted range, for all glumaceous rusts with one exception are heteroecious, and the chances, therefore, to detect and prove the genetic connection would be few. I have found that corn rust continues to produce uredospores until very late in the fall, in fact often as long as the corn plants are alive. On October 9, 1901, I tested uredospores taken from plants in the field partly killed by frost, and found that they germinated well in drop cultures. It would seem possible for the rust in northern regions to be wholly distributed by uredospores, beginning in spring from a locality sufficiently far southward to permit the corn plant to survive the winter. However, all these ruminations have taken on a different aspect by the discovery of the aecidium.

The preliminary observations, which provided the necessary inference on which successful cultures were founded, were essentially of the same character as those connected with three-fourths of the discoveries in heteroecism which I have so far made, and are therefore given in some detail as a typical and suggestive example of the method employed in my work.

On June second of the present year, while walking through a thick growth of weeds bordering a cultivated field, I came upon some plants of *Oxalis cymosa* Small, the common form of yellow wood-sorrel in this region, bear-

ing aecidia. The weeds were over two feet high, mostly *Ambrosia trifida*, with many small plants of other species beneath, the Oxalis being abundant. As this aecidium is rarely collected, I began to gather herbarium specimens, and observed that while nearly every leaf on the lower half of the Oxalis stems was infected with the rust over an area of about three feet in diameter, beyond that area it grew less frequent, and was quite absent in four or five feet from the center of the infected area, although the Oxalis plants were equally abundant everywhere in the vicinity. It seemed to me this gave evidence that the teleutosporic source of infection was within the narrow limits of the rusted area. I reasoned that if the sporidia had been blown from a distance, the infection would have been more evenly distributed, and over a larger area. I observed that the lowest leaves on the plants were most thickly dotted with aecidia, and especially those caught beneath the tangle of dead stems from last year's growth. This indicated that the germinating teleutospores must have lain close to or upon the ground, and that the protecting weeds and shrubs had prevented currents of air from materially distributing the sporidia.

I now instituted a search for remains of sedge or grass which might happily show a few teleutosporic sori. Usually one is embarrassed by finding portions of many species, often unidentifiable, but in this case I could find no clumps or stalks of sedge or grass within the infected area, apparently none having grown the previous season, doubtless prevented by the dense thicket of tall weeds, or else they had wholly disintegrated. There was, however, quite a mass of débris deposited by the spring over-flow of the near-by river, made up largely of broken cornstalks, but so covered with silt that it was impossible to tell if they had borne rust or not. The cornstalks did not occur beyond the affected area, and so were seized upon as a possible, although very dubious, clue.

The task of testing this inference was neither difficult nor protracted, a piece of good fortune but rarely encountered. Rusted leaves of the Oxalis were taken to the laboratory, about two miles distant, their long petioles placed in a vial of water, and adjusted over a potted plant of corn (*Zea Mays* L.), the whole being covered with a bell jar. On the third day the bell jar was removed.

On the fifth day the corn leaves appeared paler where the spores had presumably fallen; on the seventh day watery pimples began to show; and on the eighth day a few uredosori had opened. In a day or two more hundreds of characteristic sori were displaying a wealth of fuscous spores; and nearly the whole green area of the leaf blades, upon both sides, was so thoroughly rusted as to threaten the life of the tissues.

This prompt and very abundant appearance of the uredo could be interpreted only as the result of the aecidial infection, for corn rust had not yet appeared out of doors, and even if it had, such an unusual attack following closely within the time limit of incubation would be highly improbable. It may therefore be considered proved that the aecidium of *Puccinia Sorghi* Schw. occurs upon Oxalis, and a verification with teleutosporic material can be confidently undertaken in due time.

There are but seven or eight records in literature of the collection of aecidia on Oxalis, and there is little doubt, if any, that in every case the aecidium belonged to *Puccinia Sorghi*. They are as follows:

1876. Collected on *Oxalis Bowiei* Lindl. near Somerset East, Cape Colony, South Africa, by P. MacOwan, and issued in Thuemen's *Mycotheca universalis*, no. 1226. It was given the name of *Aecidium Oxalidis* by Thuemen and described as a new species in Flora **63**:425. 1876. I have seen several specimens from this collection, and can detect no morphological difference between the African fungus and the one from which I raised uredospores. The probability of its being the same species is somewhat increased by the fact that *Puccinia Sorghi* Schw. on cultivated corn was also found near Somerset East by the same collector (Flora **63**:569. 1876) in the preceding autumn.

1877. Collected on *Oxalis violacea* L. at Ames, Iowa, by the writer (Bull. Iowa Agric. College —:167. Nov. 1884). Only a few affected leaves were found.

1887. Collected on *Oxalis stricta* L. at Manhattan, Kan., by W. A. Kellerman (Eliss & Everhart's North Amer. Fungi, no. 2210) and M. A. Carleton (Bartholomew's Kansas Uredineae in Trans. Kans. Acad. Sci. **16**:190). These citations probably represent only one collection. The specimen in N. A. F. agrees with the Indiana collection, except that the host is a different though closely related species.

1889. Collected on *Oxalis violacea* L. at Lincoln, Neb., by H. J. Webber (Bull. Neb. Agric. Exper. Sta. no. 11:333, and Rep. Neb. Bd. Agric. **1889**:211), who speaks of it as rare; and also on the same host at Weeping Water, Neb., about 50$^{km}$ from Lincoln, by T. A. Williams (Rep. Neb., Bd. Agric. *l. c.*), who reports it as common. I have not seen these collections.

1893. Collected on *Oxalis corniculata* L. at Bozen in the Austrian Tyrol, by J. Peyritsch. This was published by Dr. P. Magnus in the Innsbruck Naturw.-Med. Verein reports for 1894, and described as a new species with the name *Aecidium Peyritschianum*. I have not seen a specimen from this collection, or the published article, but I do not doubt that

the name is a synonym of *Aecidium Oxalidis* Thuem., judging from the brief description in Saccardo's Syll. **11**:215, and from the fact that corn is grown in the region where the fungus was found.

1893. Collected on *Oxalis stricta* L. at Lincoln, Neb., by the Botanical Seminar (Bot. Survey Neb. **3**:10). I have not seen the collection.

1894, 1899. The herbarium of the writer also contains a collection made by Mr. T. A. Williams on July 13, 1894, at Brookings, S. D., and one by Mr. E. Bartholomew on June 5, 1899, in Rooks county, Kan., both on *Oxalis stricta* L., of which there is no published record.

Summing up the evidence, the writer believes that all the above collections can be placed with much confidence under *Puccinia Sorghi* Schw., as representing the aecidial stage of the fungus. It would be interesting to discuss the change in views which this discovery of the aecidium must produce regarding the propagation and dissemination of corn rust, but that can better be left for another occasion.—J. C. ARTHUR, *Purdue University, Lafayette, Ind.*

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## AN EXPERIMENT ON THE RELATION OF SOIL PHYSICS TO PLANT GROWTH.

### CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LX.

#### (WITH THREE FIGURES)

IN studies of the relation of soils to vegetational distribution in Michigan,[1] one of the authors found reason to believe that the nature of the vegetation covering any upland area of that region has been determined by the amount of water present in the surface layers of the soil. Furthermore, it was pointed out that, with the exception of swamp margins, the amount of water thus present is dependent upon the physical nature of the soil, especially upon its water-retaining or capillary power, which, in turn, is largely dependent upon the size of the soil particles. The physics of this proposition, together with the literature thereon, is discussed in a paper about to appear in the Annual Report of the Michigan Board of Geological Survey for 1903. It will be necessary to state here only the general fact that the smaller the particles of a soil, the greater will be its water-retaining power, and the larger the particles, the smaller this property. Also, the greater the retaining power, the greater will be the power to lift water from a lower level. Thus, clay soils have a great power of

[1] LIVINGSTON, B. E., The distribution of the plant societies of Kent county, Michigan. Ann. Report Michigan Board of Geol. Survey, 1901.

The distribution of the upland plant societies of Kent county, Michigan. BOT. GAZ. **35**:36–55. 1903.

retaining and lifting water, while sandy soils possess this property to a much less degree.

Since the natural soils dealt with in the paper cited differ chemically as well as physically, clay being largely composed of alumina and sand of silica, it seemed wise actually to test by field cultures the hypothesis above referred to. It was desirable that in these cultures the several soils should at the start be chemically the same, while their physical properties alone
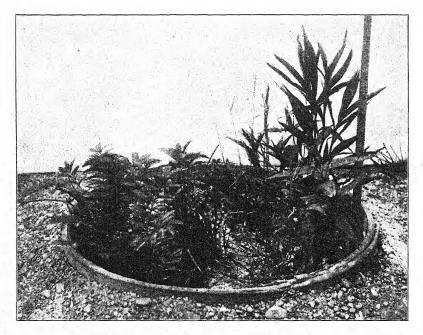


Fig. 1.

should differ. To this end crushed quartz, containing 99.8 per cent. pure silica, was obtained in three sizes or grades. The particles of the finest grade have an average diameter of $0.02^{mm}$; those of the medium $0.6^{mm}$; and those of the coarse $1.15^{mm}$. To these different sands were added mineral salts which should supply the essentials for plant growth. The proportion of the ions to the volume of soil was made approximately the same as it was found to be in natural fertile soils by Taylor and Mooney.[2] The salts actually used were $KH_2PO_4$, $Ca(NO_3)_2$, $MgSO_4$, $NaNO_3$. and $CaCl_2$. All three grades of sand were treated exactly alike.

Three ordinary apple barrels were chosen for the cultures. These

[2] U. S. Dept. of Agric., Bureau of Soils, Bull. 22:37. 1903.

have an end diameter of 40$^{cm}$ and a height of 70$^{cm}$. After a number of
holes had been bored in the sides and bottom, each of these was placed
upright, with the top even with the general ground surface, in gravelly
sand of an ancient lake beach in the experiment grounds of this laboratory.
The barrels stand in a north-and-south row about a meter apart, the finest
soil being at the southern end of the row, the coarsest at the northern.
Each barrel was filled to the brim with its particular grade of culture soil,
the salts being added in solution as the sand was shoveled in. The soil in
and around the barrels was then thoroughly soaked with water. After the
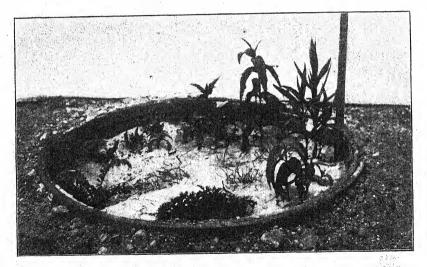


FIG. 2.

soils thus prepared had stood several days, wild plants were dug in the
vicinity of the university and set out in the cultures, practically all of the
soil adhering to their roots having first been removed by gentle water-
washing.

Similar plants, from the same locality, and often from the same clump,
were chosen for the cultures. Immediately following the planting, suffi-
cient water to wash the soil closely around the roots was added and no
subsequent watering was done. The plants used are as follows: *Poa
compressa, Poa pratensis, Potentilla anserina, Potentilla argentea, Solidago
serotina, Helianthus strumosus, Helianthus divaricatus, Verbena stricta,*
and *Verbena hastata.*

Placed in the open, as the cultures are, they have been subjected to
the same external moisture conditions both in regard to precipitation and

absorption from the surrounding natural soil. At the time of placing the barrels, the ground water of the ridge where they were sunk had its surface at a depth of $2.2^m$, *i. e.*, $1.5^m$ below the bottom of the barrels. Thus the three cultures present no differences either in external water or in chemical nature, but differ only in size of their component quartz particles. It need hardly be added that the gravelly sand surrounding the barrels is perfectly uniform throughout the series.
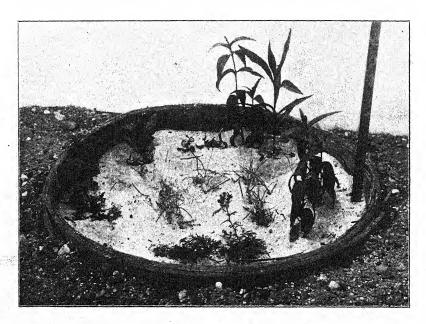


FIG. 3.

The cultures were started May 5, 1904. For the first few days no difference was to be noted in the growth of the plants, but gradually those in the finest sand forged ahead of the others, and on June 5 a difference was very well marked. The plants in the finest material showed a much greater growth and a greater general thriftiness of vegetation. The photographs here presented exhibit clearly the relation between the three cultures as they existed on June 15. *Fig. 1* shows the condition of the culture in fine sand; *fig. 2*, that in medium sand; and *fig. 3*, that in coarse sand.

The following table shows the height in centimeters of the plants in the three cultures on June 15.

| Plant | Fine soil | Medium soil | Coarse soil |
|---|---|---|---|
| Potentilla anserina............ | 20–23 | 8–10 | 6– 8 (3 out of 4 dead) |
| Potentilla argentea............ | 20–23 | 4– 5 | 3– 6 |
| Verbena stricta............... | 8–15 | 2– 5 | 2– 4 |
| Verbena hastata.............. | 14–19 | 5– 8 | 2– 3 |
| Solidago serotina............. | 42–45 | 10–17 | 10–12 |
| Helianthus strumosus ........ | 18–23 | 3–12 | 10–11 |
| Helianthus divaricatus ........ | 22–28 | 14–19 | 10–17 |
| Poa pratensis ............... | 15–20 | dead | dead |
| Poa compressa............... | 28–40 | nearly dead | dead |

While the above table is strikingly significant in showing relative size, and therefore relative rate of growth, it does not express at all the equally prominent features of comparative size and numbers of leaves, the presence or absence of runners, the wealth or scarcity of flowers, and all the features which go to make one plant vigorous and the other barely existing.

It will be realized at once that the experiment here described offers somewhat conclusive evidence in favor of the above-mentioned hypothesis of one of the present authors (*loc. cit.*), as well as of that recently expressed by Whitney and Cameron[3] in regard to agricultural plants. A fuller discussion and analysis of the conditions here dealt with would be out of place in this announcement, the purpose of the latter being only to state the facts in regard to the experiment. Further work along these lines is in progress.—BURTON EDWARD LIVINGSTON and GERHARD H. JENSEN, *The University of Chicago.*

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## A NEW GILIA.

**Gilia sapphirina**, sp. nov. (HUGELIA).—Erect, paniculately branched from the base, the branches slender, sparsely leaved, the main stem and some of the principal branches inclined to be tortuous, viscid-glandular throughout, $30^{cm}$ high or more: leaves (all but the uppermost) simple, subterete, tipped with a white bristle, often purplish, $1$–$5^{cm}$ long; uppermost leaves with two very short bristle-tipped divisions at base: flowers solitary or capitate in few-flowered clusters from most of the leaf axils, even those near the base of the stem, either sessile or on peduncles $10$–$15^{mm}$ long; involucral bracts broadly ovate and simple or 3-lobed, membranous on each side of the broad green rib, glandular and clothed with very few woolly hairs· calyx $8^{mm}$ long, the divisions one-third the entire length, the central green rib $0.75^{mm}$ wide, slightly narrower than the membranous

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[3] WHITNEY, M., and CAMERON, F. K., The chemistry of the soil as related to crop production. U. S. Dept. of Agric., Bureau of Soils, Bull. 22:72. 1903.

fold between, glandular-puberulent and viscid, not at all lanate: corolla salverform, the tube $4^{mm}$ long, slightly surpassing the spine-tipped triangular divisions of the calyx; border sapphire blue, throat yellowish, lobes broadly obovate to orbicular, retuse at apex, $7^{mm}$ wide, $10^{mm}$ long; filaments and anthers white, exserted about $7^{mm}$, the anthers oblong, sagittate, $3^{mm}$ long: style longer than the filaments but not equaling the anthers; stigmas 3 or 4, short, narrowly linear: capsule barely surpassing the calyx lobes, usually with only one seed in each cell, the other ovules present but abortive.

Type collected November 1903 by Mrs. Blanche Trask, in the San Jacinto Mountains, California. Specimen 2630 of H. M. Hall's collection from the same mountains, distributed as *G. virgata* Steud., is the same but is much younger than Mrs. Trask's specimen. Neither can be properly referred to *G. virgata* if the figure in Hooker's *Icones* 200 represents that species. The paniculate instead of virgate habit, the glandular instead of white-lanate pubescence, the distinct and broad membranous sinus of the calyx, the broad retuse lobes of the corolla, the few seeds in the capsule, all serve to distinguish them.—ALICE EASTWOOD, *California Academy of Sciences. San Francisco.*

# CURRENT LITERATURE.

## BOOK REVIEWS.

### Alaskan cryptogams.

THE FIFTH volume of the series presenting the scientific results of the Harriman Alaskan Expedition is devoted to papers on cryptogams.[1] It has been prepared under the general direction of Dr. William Trelease, who distributed the material to specialists and writes an interesting introduction to the volume. Dr. Trelease also shares with P. A. Saccardo and C. H. Peck in the section on fungi; the lichens are treated by Miss Clara E. Cummings, with admirably simple keys; the algae by DeAlton Saunders; mosses by J. Cardot and I. Thériot; sphagnums by C. Warnstorf, whose determinations have been edited by Trelease; the liverworts by A. W. Evans; and the pteridophytes by William Trelease.

Three of these papers, those on algae, mosses, liverworts, have already been printed in the *Proceedings* of the Washington Academy of Sciences. In this volume they are reprinted from the same electrotype plates, even to typographical errors. The utmost care has been taken to preserve the original pagination and plate numbers, so that from this volume the original publication may be quoted— a bibliographical precaution which deserves thankful recognition. It would be impossible to praise too highly the typographical elegance and beauty of this volume. No detail has been overlooked. Paper, letter-press, plates, and binding combine to make it an example of the best work of American book-makers.

And the contents, judging by the reputation of the authors of the various papers, is worthy of the perfect dress. About 75 species and 35 subspecies and varieties are described as new. Many are illustrated upon the 44 plates, of which those for fungi are colored. The clever and artistic head pieces were designed by Mr. F. A. Walpole, whose recent untimely death robs the Department of Agriculture of its most skilful botanical artist.

The phanerogams are to be presented in two volumes, under the editorship of Mr. F. V. Coville, which are announced for the present year.

Mr. Harriman deserves the cordial thanks of naturalists, not only for the expedition itself which extended so much the knowledge of the Alaskan region, but also for the sumptuous style in which he makes it possible for the results to be presented.—C. R. B.

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[1] J. CARDOT, CLARA E. CUMMINGS, ALEXANDER W. EVANS, C. H. PECK, P. A. SACCARDO, DEALTON SAUNDERS, I. THÉRIOT, AND WILLIAM TRELEASE, Alaska. Vol. V. Cryptogamic botany. Harriman Alaska Expedition, With cooperation of Washington Academy of Sciences. Imp 8vo. pp. x+424. *pls. 43.* New York: Doubleday, Page & Co. 1904. $5.00.

# NOTES FOR STUDENTS.

KOERNICKE finds that Roentgen rays, after first accelerating growth for a brief period, as do many injurious agents, later retard it.[2] Experiments with radium bromid[3] inclosed in glass, so that only the $\beta$ and $\gamma$ rays acted ($\alpha$ rays and the gaseous emanation being stopped by the glass), showed a strong retardation of the growth of seedlings, but no fatal injury. Somewhat similar inhibition of growth occurred with certain fungi after prolonged action of the rays.—C. R. B.

HARVEY[4] has made a study of the physiographic ecology of Mount Ktaadn, tracing the origin and development of the flora and noting the various factors operative in determining the present plant physiognomy. He also shows that the accepted principles of physiographic ecology hold in general in alpine as well as in lowland regions. The associations discussed are the crustaceous lichens, the reindeer moss, the alpine-tundra, the "Krummholz," the Picea-Abies forest, the "roches moutonnées," the pioneer stage of the alpestrine meadows, the meadow stage, the shrub stage, ponds, and sphagnum bogs.—J. M. C.

BOODLE[5] has made an experimental study of the ecological anatomy of the leaves of Pteris. Leaves grown in dry and exposed situations are xerophytic and have a "hypoderm;" while those sheltered and shaded are of the "shade-leaf" type, having no hypoderm and either weakly developed or no palisade tissue. The same differences were developed by different leaves of the same plant, and by different parts of the same leaf. A plant grown first in a damp greenhouse and then in the garden produced shade-leaves in the former and sun-leaves in the latter. It was further noted that the mature type of structure is not determined at an early stage in the growth of the leaf.—J. M. C.

SEWARD[6] considers the Carboniferous, Rhaetic, and Wealden floras of South Africa in an important paper. The Ecca beds are held to correspond in a general way with the Upper Carboniferous of the northern hemisphere, and are more definitely correlated with the Karharbári beds of the Lower Gondwana in India. Evidence from the contained plants emphasizes the well-known similarity which existed during the Carboniferous between the floras of India, South

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[2] KOERNICKE, MAX, Ueber die Wirkung von Röntgenstrahlen auf die Keimung und das Wachsthum. Ber. Deutsch. Bot. Gesells. **22**:148–155. 1904.

[3] KOERNICKE, MAX, Die Wirkung der Radiumstrahlen auf die Keimung und das Wachsthum. *ibid.* 155–166. *pl. 10.* 1904.

[4] HARVEY, LE ROY HARRIS, A study of the physiographic ecology of Mount Ktaadn, Maine. The University of Maine Studies, no. 5. pp. 50. *figs. 6.* Dec. 1903.

[5] BOODLE, L. A., The structure of the leaves of the bracken (*Pteris aquilina* Linn.). Jour. Linn. Soc. Bot. **35**:659–669. 1904.

[6] SEWARD, A. C., Fossil floras of Cape Colony. Ann. S. African Museum **4**: 1–116. *pls. 14. figs. 8.* 1903.

Africa, and South America. The Stormberg beds are considered as of Rhaetic age, and four new species are described. The Uitenhage beds are considered as probably of Wealden age, and the fragmentary remains of nineteen species of plants are enumerated, of which two, a Nilssonia and an Araucarites, are described as new.—EDWARD W. BERRY.

REED[7] has made a cytological study of enzyme-secreting cells in corn and date seedlings. Sections of living tissue were compared with fixed material to avoid error. Torrey's technique[8] is regarded faulty, and no evidence was found to support his observation that solid matter extrudes from the nucleus through interruptions of the nuclear membrane into the cytoplasm. In addition to a careful study of the literature and some valuable data in technique, the observations of special interest are: "(1) In the resting condition the secreting cells of both Zea and Phoenix are crowded with relatively small proteid granules. As secretion begins these granules gradually disappear. In Zea this disappearance coincides closely with consumption of the endosperm; in Phoenix, however, the granules disappear long before the endosperm is dissolved. (2) The chromatin of the nucleus is small in amount at the beginning of secretion and increases as germination progresses. These changes are more noticeable in the case of Zea than in Phoenix."—RAYMOND H. POND.

WIELAND[9] has brought together a large array of facts to support the thesis that polar climate has been the major factor in the evolution of plants and animals. He shows that climatic changes of a character affecting life must in the course of time be at a minimum at the equator and at a maximum at the poles. He also thinks it reasonable that the origin of life itself took place at the north or at both poles; and that the Palaeozoic for various reasons was a period mainly of "generalized origins." From the origin of life down to the Mesozoic the north and south polar areas may have played a well-nigh equal part in creating a certain southward and northward stress; but beginning with the Mesozoic and "extending to the glacial period, overwhelming evidence points to the polar origin and continuous outward dispersion from the north polar area of most of the great plant and vertebrate groups." Among the illustrations of this the author calls attention to "the outward movement especially of conifers and dicotyls from the Arctic area for long periods of time."—J. M. C.

WAGER,[10] in a preliminary paper, has discussed the much debated question of the cell structure of the Cyanophyceae. He concludes that the central body

[7] REED, H. S., A study of the enzyme-secreting cells in the seedlings of *Zea Mais* and *Phoenix dactylifera*. Annals of Botany 18:267. 1904.

[8] TORREY, Cytological changes accompanying the secretion of diastase. Bull. Torr. Bot. Club 29:421. 1902.

[9] WIELAND, G. R., Polar climate in time the major factor in the evolution of plants and animals. Am. Jour. Sci. IV. 16:401–430. 1903.

[10] WAGER, HAROLD, The cell structure of the Cyanophyceae. Preliminary paper. Proc. Roy. Soc. 72:401–408. 1904.

is a nucleus of a "simple or rudimentary type," although not to be regarded as one of normal type, similar to the nuclei of the higher plants. He enumerates twelve main chemical and morphological characters that belong to the nuclei of higher plants, and claims that at least seven of them belong to the central body of the Cyanophyceae, as follows: (1) presence of a nuclear network, (2) reaction to nuclear stains, (3) behavior toward digestive fluids, (4) presence of phosphorus, (5) presence of masked iron, (6) amitotic division, and (7) presence of chromatin granules on a linin framework. It differs from the nuclei of higher plants in the absence of a true mitosis with spindle fibers, and in the absence of a nuclear membrane and a nucleolus, although in certain conditions both membrane and nucleolus are said to be suggested. The author evidently regards this central body as a developmental stage in the evolution of the nucleus of higher plants.—J. M. C.

BECAUSE of their perishable nature fungi are rare as fossils, and yet Weiss[11] finds the remains of a parasitic fungus on stigmarian rootlets from the Lower Coal Measures. Magnus has compared this type with the existing Urophlyctis, which it resembles not only in so much of its structure as is discernible, but also in its similar habit of growing on plants which inhabit marshy or at least wet situations. Weiss accords in this identification to the extent of naming the fossil *Urophlyctites Stigmariae.*

The same author[12] notes a mycorhiza from the same geological horizon. Janse is quoted as saying that 69 out of 75 plants in a tropical forest have their roots infested by symbiotic fungi, and while this condition argues considerable specialization on the part of both, the similar conditions that prevailed during the Carboniferous mitigates our surprise at finding symbiosis occurring so far back as this. The roots have not been associated with the plant which bore them; they are possibly lycopodiaceous and are referred to the form-genus Rhizonium of Corda. The hyphae are for the most part intracellular, but in no case is there any sign of injury to the host. The fungus is named *Mycorhizonium,* and is considered as possibly belonging to the Phycomycetes.

ZODDA[13] records the finding of a cone of a species of Pinus still living, in the Lower Pliocene of Sicily.—EDWARD W. BERRY.

A HYBRID between *Drosera rotundifolia* and *D. longifolia* was investigated about a year ago by Rosenberg.[14] He found that *D. rotundifolia* has ten chromosomes in the pollen mother-cells, while *D. longifolia* has twenty; further, that in the hybrid there are found pollen mother-cells with ten, twenty, and

[11] WEISS, F. E., A probable parasite of stigmarian rootlets, New Phyt. 3:63–68. 1904.

[12] WEISS, F. E., A mycorhiza from the Lower Coal Measures. Annals of Botany 18:255–265. *pls. 18, 19.* 1904.

[13] ZODDA, G., *Pinus Pinea* L. fossile nel Pontico di Messina. Malpighia 17: 488–492. 1903.

[14] Review in BOT. GAZ. 36:152. 1903.

fifteen chromosomes, the ten and twenty being the number characteristic of pure pollen mother-cells of the two parents, while the number fifteen is just what one would expect in the pollen mother-cells of a genuine hybrid. A recent paper[15] records the results of investigations upon the embryo sac mother-cells of the parent and the hybrid. The sporophytic cells of the hybrid always show thirty chromosomes. In the pollen mother-cells and embryo sac mother-cells, the number of chromosomes is twenty, a very surprising number. These twenty chromosomes are not alike, but of two sizes, ten being large and ten small. The large chromosomes are evidently double and the small ones single. *D. rotundifolia* is represented in the hybrid by ten chromosomes and *D. longifolia* by twenty. In the mother-cell the ten chromosomes of *D. rotundifolia* fuse with ten of *D. longifolia*, thus leaving the other ten chromosomes of *D. longifolia* single. These are the numbers as seen during the metaphase. The daughter nuclei of the tetrads contain quite regularly ten chromosomes, presumably five being single and five double. It is evident that these observations have an important bearing upon the problem of the reduction of chromosomes, and it is to be hoped that the full account of the investigations will not be long delayed.—C. J. CHAMBERLAIN.

WITH THE rediscovery of Mendel's laws by Correns, Tschermak, and De Vries, there has been a revival of interest in the fundamental problems of heredity and hybridization, and many works of both experimental and speculative character have appeared. One of the most active workers in this field is Correns. In several recent papers he has presented an account of some of his hybridizing experiments and has discussed questions of dominance.

A very striking result of experiments with Mirabilis hybrids[16] was the production of characters in the offspring, which were found in neither parent. Thus the offspring of dark yellow or pale yellow *Mirabilis Jalapa* crossed with the pure white form, never showed either yellow or white, but all were red or rose-colored. In the second generation these red-flowered hybrids gave rise to a whole series of forms, red-striped, white, pale yellow, rose, and red. Similarly *M. Jalapa* of whatever color crossed with *M. longiflora* (white with a red-violet throat), resulted in offspring having violet corollas, differing in the different cases only in the intensity of the color.

In discussing dominance[17] he points out that there may be every degree of dominance and suggests that a character be considered dominant if it occur in 75 to 100 per cent. of the offspring, and recessive if it occur in 0 to 25 per cent. of the offspring. Characters transmitted to 25 to 75 per cent. are intermediate;

[15] ROSENBERG, O., Ueber die Tetradenteilung eines Drosera-Bastardes. Ber. Deutsch. Bot. Gesells. **22**:47–53. *pl. 4.* 1904.

[16] CORRENS, C., Ueber Bastardirungsversuche mit Mirabilis-Sippen. Ber. Deutsch. Bot. Gesells. **20**:594–608. 1902.

[17] CORRENS, C., Ueber die dominierenden Merkmale der Bastarde. Ber. Deutsch. Bot. Gesells. **21**:133–147. 1903.

there is no dominance. Careful determinations of the intensity of color in parents and offspring showed that many errors have been made regarding dominance, through the neglect of Weber's law. The intensity of the color does not measure the amount of pigmentation. He concludes that complete dominance is much less common than has been supposed. In a second paper on dominance[18] he presents a number of cases which do show complete dominance; *e. g., Hyoscyamus annuus* × *niger* shows absolute dominance of the biennal habit. Rimpau found, on the other hand, that the annual habit is completely dominant in *Beta patula* × *vulgaris;* dioecism dominates monoecism in *Bryonia alba* × *dioica.* Correns opposes the statement by De Vries that dominance is characteristic of hybrids between races and that hybrids between species are intermediate. He shows that in form and color of root the hybrids between turnip races are intermediate, and he also gives examples of dominance in hybrids between distinct species. He discusses[19] the unique suggestion of De Vries that hybrids which fail to "split" in the second generation have *Anlagen* in one parent unmatched by corresponding *Anlagen* in the other, and concludes that no such condition exists, and that if no splitting occurs it is due to some other cause than that there is nothing to split.

Correns has recently reviewed[20] the present state of our knowledge of the origin of species. He presents the experimental work which has been done, laying most stress on the work of De Vries and Johannsen. The presentation is fair in the main, but one cannot avoid feeling that he begs the question as to the significance of individual variations for evolution, when he distinguishes mutations as *inheritable* variations, however slight.—G. H. SHULL.

[18] CORRENS, C. Weitere Beiträge zur Kenntnis der dominierenden Merkmale und der Mosaikbildung der Bastarde. Ber. Deutsch. Bot. Gesells. 21:95–201. 1903.

[19] CORRENS, C., Die Merkmalspaare beim Studium der Bastarde. Ber. Deutsch. Bot. Gesells. 21:202–210. 1903.

[20] CORRENS, C., Experimentelle Untersuchungen über die Entstehung der Arten auf botanischen Gebiet. Arch. f. Rassen- und Gesellschafts-Biologie 1:27–52. 1904.

# NEWS.

W. A. MURRILL has succeeded F. S. Earle at the New York Botanical Garden as assistant curator in charge of the fungi.

PROFESSOR F. L. STEVENS has been elected president of the North Carolina Academy of Science for the ensuing year.

COLUMBIA UNIVERSITY has recently conferred the honorary degree of Sc.D. upon Professor Hugo DeVries, of Amsterdam.

EDWARD W. BERRY has been elected secretary of the Torrey Botanical Club in the place of Professor F. S. Earle, who recently left for Cuba.

THE UNIVERSITY OF WISCONSIN at its recent Jubilee conferred the honorary degree of LL.D. upon Professor W. G. Farlow, of Harvard University.

D. T. MACDOUGAL, director of the laboratories of the New York Botanical Garden, has been advanced to the position of assistant director of the institution.

DR. C. C. HOSSEUS left Berlin on June 22 for a collecting expedition in Siam. The sets of plants obtained will be sold from the Royal Botanic Museum of Berlin.

A. F. BLAKESLEE of Harvard University has received a grant from the Carnegie Institution to spend next year in Europe continuing his mycological investigations.

JOHN MACOUN, the veteran botanist of the Canadian Geological Survey, will spend this summer in the Rocky Mountains of Canada making extensive collections of cryptogams.

AT THE RECENT annual meeting of the Linnean Society (London) the supplemental charter was laid before the fellows, one item of which gives authority to elect women to membership.

LAETITIA MORRIS SNOW received the degree Ph.D. at the June convocation of the University of Chicago, the subject of her thesis being "The effect of external agents upon the development of root hairs."

MEL T. COOK, formerly in charge of botany at DePauw University (Greencastle, Indiana), has been appointed plant pathologist at the Experiment Station of Cuba, newly established at Santiago de las Vegas.

THE UNIVERSITY OF GÖTTINGEN has awarded its Otto Wahlbruch prize, of the value of $3000, to Dr. Wilhelm Pfeffer, professor of botany at Leipzig. The prize is awarded for the most prominent contribution to science during the past two years.—*Science.*

MR. L. B. ELLIOTT, editor of the *Journal of Applied Microscopy* since its beginning in 1898, has severed his connection with the Bausch & Lomb Optical

Company to accept another position. He will continue his private work in laboratory photography and biology as heretofore, his address being 17 Birr Street, Rochester, N. Y.

DR. F. L. STEVENS has been promoted to the professorship of botany and vegetable pathology in the North Carolina College of Agriculture and Mechanic Arts. A new building is about to be constructed which will provide a well-equipped bacteriological laboratory, a plant-disease laboratory, and an elementary laboratory, together with offices for the professor and assistants, research rooms, and greenhouses for experimental work.

THE ANNUAL REPORT of the Secretary of the Botanical Society of America embodied in Publication 24 is a statement of conditions and record of progress during the first decade of the existence of the Society. The total constituency of the Society now numbers 58, and its accrued funds amount to nearly three thousand dollars, a large part of which is treated as permanent endowment, the income only being used. Recently the policy was adopted of making grants from current funds in aid of investigations by members and associates. Thus far grants to the amount of $840 have been made.

In order to promote unity of botanical interests a committee consisting of B. T. Galloway (chairman), C. R. Barnes, and C. E. Bessey has been appointed and requested to prepare a plan for cooperation with other botanical organizations, for consideration at the eleventh annual meeting.

The increasing demand upon the time allowed by the Society for the presentation of scientific papers has made necessary the action of the Council in accepting only papers from members, associates, and persons specially invited by the Council to contribute.

THE MANAGERS OF the Louisiana Purchase Exposition have arranged for an International Congress of Arts and Sciences, to be held in the Exposition grounds September 19–25. W. G. FARLOW, Harvard University, will preside over the general section of *Biology*, before which the speakers will be JACQUES LOEB, University of California, and JOHN M. COULTER, University of Chicago. HUGO DE VRIES, University of Amsterdam, will be one of the speakers before the sub-section of *Phylogeny*. For the strictly botanical sub-sections the following appointments have been made. *Plant Morphology:* chairman, WILLIAM TRELEASE, Washington University, St. Louis; speakers, FREDERICK O. BOWER, University of Glasgow, and KARL F. GOEBEL, University of Munich; *Plant Pathology:* chairman, CHARLES R. BARNES, University of Chicago; speakers, JULIUS WIESNER, University of Vienna, and BENJAMIN M. DUGGAR, University of Missouri. *Plant Pathology:* chairman, CHARLES E. BESSEY, University of Nebraska; speakers, JOSEPH C. ARTHUR, Purdue University, and another to be selected. *Ecology:* chairman, CONWAY MACMILLAN, University of Minnesota; speakers, OSKAR DRUDE, Königl-Technische Hochschule, Dresden, and CHARLES FLAHAULT, Director of the Botanic Institute, Montpellier, France. *Bacteriology:* chairman, HAROLD C. ERNST, Harvard University; speakers, EDWIN O. JORDAN, University of Chicago, and THEOBALD SMITH, Harvard University.

# BOTANICAL GAZETTE

## *AUGUST, 1904*

### OOGENESIS IN VAUCHERIA.

#### CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXI.

BRADLEY MOORE DAVIS.

#### (WITH PLATES VI AND VII)

THERE have been published two accounts of the development of the oogonium of Vaucheria, attempting to explain in fundamentally different ways the final uninucleate condition of the structure at the maturity of the egg. All authors have found the young oogonium multinucleate, and the problem has concerned the history of these nuclei as the egg developed and the oospore matured. BEHRENS ('90), in partial agreement with SCHMITZ's opinion that the material discharged from the opening of the oogonium represented a polar body, believed that the final single nucleus of the egg resulted from the fusion of numerous nuclei in the oogonium. KLEBAHN ('92, p. 237), in criticism of the results of SCHMITZ and BEHRENS, held that the egg and oospore were multinucleate. OLTMANNS ('95) came to very different conclusions. He described the gradual withdrawal of all the numerous nuclei found in the young oogonium from that structure into the main filament, with the exception of one which was left to become the nucleus of the egg.

The view of BEHRENS was in general similar to those of HUMPHREY and HARTOG for Saprolegnia, since the latter writers believed that the numerical reduction of the nuclei in this form was the result of successive nuclear fusions. The explanation of OLTMANNS has no parallel in any process of oogenesis known to the writer. Neither of these accounts seems to be correct, and the processes of oogenesis

in Vaucheria are along very different lines, namely those of nuclear degeneration, which are in sympathy in all essentials with the events now known for gametogenesis in Saprolegnia (DAVIS '03), several members of the Peronosporales, and certain Ascomycetes.

These facts give a high degree of interest to Vaucheria, which becomes the greater in view of the position which this form takes in the phylogenetic systems of many authors as representing a possible point of origin of the Phycomycetes. This subject will be considered, with its bearings upon the writer's theory of the origin and evolution of the coenogamete, at the end of the paper, under the head of "Theoretical Considerations."

The material, identified as *Vaucheria geminata racemosa*, was collected at Chicago, the younger oogonia being abundant late in March and older stages a week or so later. Of the killing fluids employed, chromacetic acid after the formula of FLEMMING proved to be much the most satisfactory (1 per cent. chromic acid $25^{cc}$, 1 per cent. acetic acid $10^{cc}$, and water $65^{cc}$). This formula is $\frac{1}{4}$ per cent. chromic acid and $\frac{1}{10}$ per cent. acetic acid. Chromic acid in excess of $\frac{1}{2}$ per cent. produced serious shrinkage. The weaker solution of iridium chlorid and acetic acid (Eisen) also gave fair results ($\frac{1}{2}$ per cent. iridium chlorid and 1 per cent. acetic acid). The cytoplasmic structure and plastids were perhaps better preserved in the latter fluid, but the nuclei did not stain so readily. All mixtures with osmic acid were objectionable, because the protoplasm of Vaucheria is filled with oils and fats which became so seriously blackened that they could not be thoroughly bleached. Chromic acid takes out much of these troublesome substances, or at least leaves the material so that it can be readily cleared. Paraffin sections were cut $5\,\mu$ thick and stained with safranin and gentian violet. The nuclei are so minute as to require the best of lenses, and the Zeiss apochromatic objective $1.5^{mm}$ with the compensating oculars was used entirely.

The oogonia are somewhat variable in number (2–6) and are arranged in a whorl near the end of short lateral branches just below the terminal antheridium. They commence their development as small protuberances which from the beginning are multinucleate (*fig. 1*). As growth proceeds the process enlarges and takes a globular form on the end of a short stalk (*figs. 2–4*). It is evident that

the enlargement is accompanied by a stretching of the cell wall, which
is always much thinner about the young oogonium than around the
stalk and vegetative filament, a fact which is clearly shown in *figs.
4, 5, 6,* and *7.* The growth of the oogonium results from the accumu-
lation of large amounts of protoplasm with numerous nuclei and
chloroplasts, together with the formation of vacuoles which flow
together, so that finally the protoplasm lies peripherally around a
central space crossed by a few delicate strands and films of proto-
plasm.

The number of nuclei is variable, but always large; the range is
probably from about 20 to 50. These nuclei are carried into the
developing oogonium by the accumulation of protoplasm. They
lie very close together at the tip of the young structure (*fig. 1*), but
become scattered as growth proceeds, agreeing in this respect with
the conditions found in all the growing points of Vaucheria. I have
seen no indication of nuclear division in the oogonium, and am
positive that it does not occur in stages as old or older than those
shown in *figs. 2* and *3.* It is quite probable that mitotic figures are
present in the vegetative branch before the development of the
oogonia, but I have never seen the spindles. The nuclei are so very
small and the plastids so numerous that studies of nuclear division
in Vaucheria will be very difficult. It is important to note that there
are no mitoses during the growth of the oogonium and none after
its separation by the cross wall from the parent filament. In these
respects oogenesis in Vaucheria is somewhat different from the pro-
cesses as known in Saprolegnia and the Peronosporales, where there
seem to be always one or two general mitoses after the oogonium is
formed. The absence of nuclear divisions during oogenesis in
Vaucheria presents serious difficulties for the theories of some authors
that such mitoses indicate reduction phenomena in those fungi where
they have been most studied. These speculations have been recently
criticised by the writer (DAVIS '03, pp. 339–342) and the subject will
be further considered later in this paper.

We will now describe he development of the cross wall by which the
oogonium is separated from the parent filament. It appears when the
oogonium is about two-thirds its mature size. The wall is laid down
between two plasma membranes, as was shown by HARPER ('99) for the

formation of sporangia in Pilobolus and Sporodinia, and by DEAN
SWINGLE ('03) in Rhizopus and Phycomyces. The plasma membranes
are formed chiefly along the surfaces of flattened vacuoles. I have
seen no evidence of furrows cutting inward from the surface as takes
place in Pilobolus and Rhizopus, but such structures would not be
seen easily in Vaucheria because the stalk is rather narrow. *Fig. 4*
illustrates an arrangement of vacuoles at the base of an oogonium
which would probably have determined the position of the cross
wall, and *fig. 5* shows a more advanced condition when the plasma
membranes have definitely separated from one another. The stages
shown in *figs. 6–8* are all somewhat older than that of *fig. 5*, and
there is evidence in all of them that the wall has began to form as a
delicate film visible at certain points between the two plasma mem-
branes.

The oogonium at the time of the formation of the cross wall is
multinucleate. There is no evidence in my material of the with-
drawal of nuclei from this structure, as described by OLTMANNS,
before the wall is laid down, and my preparations indicate that the
oogonium contains as many nuclei immediately after the formation
of the wall as before. These conditions are shown in *figs. 5–7*.
The number of nuclei is always large, but is variable, ranging from
20 to 50. They may be readily demonstrated at this period when
properly stained, but are very difficult to trace from this stage of
development onward because of the remarkable and rapid nuclear
degeneration which sets in at this time. This interesting phenomenon
is apparently exactly the same as that which takes place at closely
corresponding periods of oogenesis in Saprolegnia and in several of
the Peronosporales.

The degeneration of the nuclei really begins a little before the
oogonium is separated from its parent filament. At that time the
nuclei in the oogonium do not stain as strongly as those in the anthe-
ridium and in neighboring portions of the vegetative filament. The
nuclear membrane is less distinct and there is very little substance
in the nucleus except the large nucleolus. *Fig. 9* presents a series of
nuclei from the same section of which *fig. 7* is a single oogonium.
In *fig. 9, a* is a nucleus from the antheridium, *b* from a region of the
branch slightly below the antheridium, *c* from near the oogonium,

and *d* from within an oogonium.   It will be seen that *a*, *b*, and *c* are nuclei which, although small (magnified 2,000 diameters), present the structure of the nuclei of higher plants; that is, each has a nucleolus lying among granules of a chromatic nature and linin.   In *c* these structures are less conspicuous than in *b*, while *d* shows unmistakable signs of degeneration, for its nuclear membrane appears very faint and there is scarcely any trace of chromatin or linin.   The nucleolus, however, is generally large and stains deeply and is always the last structure in the nucleus to disappear.   *Figs. 6* and *7* show degenerating nuclei in oogonia shortly after the formation of the cross wall.

. It is very difficult to trace the degeneration and final dissolution of the numerous nuclei in the oogonia, because we are dealing with structures that become more and more difficult to stain and find. It becomes in the end impossible after the nuclear membrane disappears and the nucleolar material is scattered throughout the cytoplasm.   These baffling conditions are identical with those in the oogonium of Saprolegnia which the author has recently described (DAVIS '03, p. 239).

The mature oogonia are finally uninucleate.   There seems to be no doubt of this condition, and the factors governing the selection and survival of the fortunate nuclei are of interest.   We know that the process in Saprolegnia (DAVIS '03, p. 239–243) is intimately connected with the presence of organized structures in the protoplasm, the coenocentra, which are probably the morphological expression of dynamic centers.   I have not been able to find a coenocentrum in Vaucheria.   It is possible that the plastids might obscure such a structure, but this is not likely unless it were very small.   But there are conditions around the surviving nucleus in the oogonium which closely resemble those of the Saprolegniales and Peronosporales.

Before the formation of the cross wall the protoplasm in the oogonium is arranged quite irregularly.   There is always the rather thick peripheral layer just inside the cell wall, but the interior region generally contains several irregular vacuoles which frequently open into one another.   These conditions are partially shown in *figs. 3–5*, but of course they can be understood only by the examination of a number of consecutive sections.

After the formation of the cross wall, the arrangement of the cell contents becomes more regular. The oogonium increases rapidly in size, and the peripheral layer of protoplasm grows proportionally thinner. The strands and films of protoplasm that before crossed the oogonium irregularly become arranged so that there is a gradual accumulation of the protoplasm in the center of the cell, held in position by delicate strands which pass to the periphery, and the surviving nucleus always lies within this region. *Figs. 10–12* illustrate these conditions as they appear in thin sections ($5\,\mu$), but they cannot show the numerous radiating strands that hold the central mass in place. The degenerating nuclei lie chiefly in the peripheral layer of protoplasm, but some may always be found in the larger strands that enter the interior of the oogonium.

Although I have not been able to find any morphological evidence which would indicate that this accumulation of protoplasm is a dynamic center of the cell, there are good reasons for thinking that it really is such. The surviving nucleus of the oogonium is always found in this central mass surrounded by plastids and deeply staining granular protoplasm, which suggests material of a trophoplasmic nature. The peripheral protoplasm forms a thin layer under the cell wall in which one may find for a long time traces of the other nuclei that have degenerated. *Figs. 10* and *11* show some of these nuclei (*d*) so far reduced that there is nothing left but a deeply stained (with safranin) globule of nucleolar material apparently lying free in the protoplasm. No one would relate these structures to nuclei unless he had followed their history through the process of degeneration, for they are soon reduced almost beyond the point of recognition. But at this time the surviving nucleus (*fig. 10*) near the center of the oogonium increases rapidly in size until in the mature egg (*fig. 11*) it is three or four times as large as the original nuclei in young oogonia. The inference is plain that the central region of the oogonium is a much more favorable situation for nuclear growth and activities than at the periphery.

For this reason the author considers the dense central mass of protoplasm as comparable to the region of the egg in Saprolegnia and the Peronosporales which is dominated by the coenocentrum. It is apparently the region of the cell most favorable for nuclear

growth and activity, and as such is a dynamic center. There is a very close resemblance to certain of the Peronosporales (*e. g.*, Pythium) whose oogonia have merely an accumulation of dense protoplasm in place of the usual well-defined coenocentrum.

The growth of the surviving functional gamete nucleus presents some interesting features. There is a marked increase in the amount of chromatin which fills the interior with numerous small granules on a very delicate linin network. The nucleolus does not increase in size, so that it appears relatively much smaller in the older nucleus than in the younger (compare *fig. 11* with *figs. 3* and *4*). *Fig. 11* is of an oogonium almost at maturity, and *fig. 12* is after fertilization and shows two gamete nuclei fusing and also the remains of three sperms which were unable to enter the egg.

The final steps in the maturation of the egg, as has been frequently described, consist in the breaking down of a portion of the wall of the oogonium and the formation there of a pore through which the sperms enter. Much slime is developed, which partially exudes from the opening. Numerous sperms are attracted to the oogonium, and one may frequently find conditions such as are shown in *fig. 13*, where the slime at the opening is filled with sperms held in the muci-laginous matrix. It is possible that such conditions were interpreted by Schmitz as nuclear material thrown off from the egg as a polar body.

The union of the gamete nuclei takes place slowly. The male nucleus increases greatly in size, apparently being nourished in the dense central region of the egg, and the great increase in the amount of chromatin is as conspicuous here as in the female nucleus. Although the male nucleus is much smaller at first than the female, the two are approximately the same size before they begin to fuse (*fig. 14*), and both show essentially the same structure at that time. As fusion proceeds the two nuclei become indistinguishable (*fig. 12*).

The history of oogenesis in Vaucheria may then be briefly described as from a multinucleate gametangium, by a process of rapid and complete degeneration of all the nuclei except one, which is reserved with all of the protoplasm for a single uninucleate egg. In these respects Vaucheria offers certain important differences and yet some fundamental points of agreement with the conditions in the Sapro-legniales and Peronosporales, which will now be considered.

### THEORETICAL CONSIDERATIONS.

The essential agreement of the processes of oogenesis in Vaucheria with those of Saprolegnia and members of the Peronosporales is most striking. The oogonium in all of these forms so far known—Vaucheria, Saprolegnia, Pythium, Peronospora, Plasmopara, Sclerospora, Albugo, and Araiospora (KING '03)—is differentiated from the parent filament as a multinucleate cell. There may be one mitosis in the oogonium (Saprolegnia), or two as in certain of the Peronosporales, or there may not be any (Vaucheria), but finally extensive nuclear degeneration always begins. From among the weakened nuclei one or more are selected to preside over the eggs. The position of these surviving gamete nuclei in relation to favorable dynamic centers of the oogonium determines their selection and leads to extensive regenerative growth. In Saprolegnia and some of the Peronosporales (*i. e.*, Albugo, Peronospora, Plasmopara, Sclerospora) the dynamic centers are marked by the protoplasmic structures called coenocentra, which are apparently trophoplasmic in character, since they exert a chemotactic influence on the gamete nuclei near them and are obviously concerned with their later growth. Although there is no coenocentrum in Vaucheria, the surviving nucleus takes its position in a central mass of protoplasm which is evidently the most favorable situation in the oogonium for its growth, and as such is a dynamic center, although there is little morphological evidence of the condition.

The fact that there are no mitoses in the oogonium of Vaucheria is seriously against the view that they have relation to reduction phenomena when present in the oogonia of Saprolegnia and the Peronosporales. I have already expressed the conviction (DAVIS '03, pp. 339–342) that these mitoses in the oogonium have no such significance, because they are so variable in their appearance and because there is no positive evidence of such functions. ROSENBERG ('03) from studies on Plasmopara believes that a synapsis condition preceding the first of the two mitoses in the antheridium and oogonium of this form indicates reduction phenomena comparable to that in the tetrad division of the spore mother-cell of higher plants. The author has recently (BOT. GAZ. 36: 154–155. 1903) criticised this view in several respects, which need not be repeated here, and the absence of mitoses

in Vaucheria offers further difficulties for such a theory.  RUHLAND
('03) is also unwilling to follow ROSENBERG in his theory of reduction.

For these reasons the writer believes that the mitoses in the oogonia
and antheridia of the Phycomycetes have no special significance, or
are merely the remains of nuclear divisions that were formerly char-
acteristic of simpler types of gametangia or perhaps the primitive
sporangia that preceded these.

The simple precesses of oogonesis in Vaucheria seem to prove
conclusively that all of the nuclei in the oogonium are homologous
and potentially gamete nuclei, and this supports HARTOG'S suggestion
for Saprolegnia of many years ago.  The author believes this to be
equally true of the nuclei in the gametangia of the Saprolegniales
and the Peronosporales.  The mitoses in the last two groups have
complicated the problem, but there seems now to be no special sig-
nificance in these divisions, since they are not only variable in num-
ber, but may be entirely absent.  Thus there are two mitoses in
Albugo and Plasmopara, but only one in Saprolegnia, certain species
of Peronospora, and Pythium, and they are entirely absent in the
species of Vaucheria just described.

There are then excellent reasons for considering all of the potential
and functional gamete nuclei in Vaucheria, Saprolegnia, and the
Peronosporales as homologous, and there seems to be little doubt
but that the oogonia of all these forms are related at least as game-
tangia through remote ancestors, if not as fully differentiated oogonia.

The problems then concern the exact relationships between the
eggs of Vaucheria, Saprolegnia, and forms of the Peronosporales.
Are these female gametes strictly speaking homologous, or have they
been developed along somewhat different paths?  An old view, and
that probably held by most botanists, is one of strict homology,
implying an intimate relationship between these fungi and Vaucheria.
It is a problem of fundamental importance in all discussions of
phylogeny in this region of the plant kingdom, and of special con-
cern to those who make Vaucheria the starting point of a series of
fungi beginning with the Peronosporales or the Saprolegniales and
ending in the Mucorales.

From all points of view oogenesis in Vaucheria is simpler than in
the Saprolegniales or Peronosporales.  It conforms perfectly to well-

known principles of sexual evolution which the author has recently discussed (*Popular Science Monthly*, February 1903, p. 300). The process represents the final stage of nuclear reduction in a multi-nucleate oogonium, and indicates plainly that the ancestral game-tangium produced numerous gametes which were undoubtedly motile, since the sperms of Vaucheria are biciliate and the Siphonales repro-duce almost universally asexually by zoospores. It is difficult to follow exactly the steps through which the ancestors of Vaucheria passed in their evolution from isogamy, because it is the only heter-ogamous type in the order, and there are few connecting links with the prevailing simple conditions among the Siphonales. However, we have in Bryopsis a form whose gametes, although both motile, are of different sizes, those of the female being much larger and developed less numerously in the gametangium. This type exhibits the first step toward the condition of heterogamy, but we do not know exactly what would follow next. Probably the protoplasmic cleavage in the female gametangium would become gradually reduced and fewer gametes formed, until finally there would be no more cleav-age, all of the protoplasm going into a single gamete, which when non-motile would become the solitary egg (Vaucheria). This con-centration of protoplasm for a lessened number of gametes or for a single egg must be accompanied by nuclear degeneration *if the ances-tral gametangium were multinucleate*. There are of course types of gametangia among the algae which are uninucleate from the begin-ning, and there cannot be any nuclear degeneration in these. But the multinucleate gametangium is not uncommon in certain groups, and is apparently universally present in the Siphonales.

It is possible that Sphaeroplea will be found to represent a stage in sexual evolution intermediate between Bryopsis and Vaucheria, without necessarily implying a relationship to these types. Klebahn ('99) and Golenkin ('99) have given us the most complete accounts of oogonesis in Sphaeroplea. Klebahn found the eggs of *S. annulina Braunii* to contain several nuclei (2–5), one of which became the functional female gamete nucleus; the others remained inactive and might be found in the ripe spore. It becomes an interesting question whether or not these would eventually degenerate. This form of Sphaeroplea may illustrate the beginning of a process by which

fewer eggs are developed than the number of gamete nuclei, but before a habit of nuclear degeneration has become fully established. It is altogether probable that the extra nuclei in the eggs of the var. *Braunii* do eventually break down.

Besides Sphaeroplea, it is very important that we know the processes of oogenesis in Monoblepharis, since this form has a structure with many points of resemblance to the algae on the one hand and the groups of Saprolegniales and Peronosporales on the other. LAGERHEIM ('oo) states that a single large nucleus enters the developing oogonium to become the gamete nucleus of the egg. Such a history is not in sympathy with oogenesis in Vaucheria and the Peronosporales or Saprolegniales, nor is it in sympathy with his own description of spermatogenesis in Monoblepharis. The antheridium contains many nuclei, each of which enters into the development of a sperm as in Vaucheria. The author cannot but think that LAGERHEIM's account of oogenesis is incorrect, or else that the conditions here are very exceptional. It seems very probable that Monoblepharis and perhaps some of the forms in the Leptomitaceae are closely related to Vaucheria.

The problem of the relationship of the events of oogenesis in the Saprolegniales and Peronosporales to Vaucheria may be stated as follows. Have the conditions in these groups been developed directly from the relatively simple process illustrated by Vaucheria, or are there peculiarities in these two groups that would make necessary their derivation from more generalized types?

The Saprolegniales present conditions that superficially bear a very close resemblance to Sphaeroplea, *i. e.*, there are several eggs in the oogonium. But these eggs are differentiated around coenocentra which determine the survival of a limited number of nuclei, while the great majority break down. There are fundamental differences between these events and oogenesis in Sphaeroplea, unless later studies should establish nuclear degeneration in the latter type. It would not be difficult to conceive the development of several metabolic centers in a large gametangium of one of the Siphonales, and the survival of several nuclei to form as many eggs which would give a condition exactly like that of Saprolegnia. So the present investigation with the discovery of a multinucleate oogo-

nium in Vaucheria tends to bring the Saprolegniales into a somewhat close relationship to Vaucheria, not directly of course, but probably through more generalized types of the Siphonales now extinct.

The Peronosporales offer a more difficult problem than the Saprolegniales, yet there are fundamental features of oogonesis here in agreement with this group and with Vaucheria, namely a multinucleate oogonium and extensive nuclear degeneration. The advance of the process of oogenesis in the Peronosporales over that of Vaucheria lies in the differentiation of ooplasm and periplasm, the first being associated with a remarkably well-developed coenocentrum. The influence of this coenocentrum determines the survival of one or more nuclei in the ooplasm to give a uninucleate or multinucleate egg. The periplasm, containing numerous nuclei, becomes separated from the ooplasm, and although assisting in the deposition of the oospore wall its nuclei and cytoplasm finally become disorganized.

The processes of oogenesis in the Saprolegniales and Peronosporales seem higher than those of Vaucheria because of the remarkable activities of the coenocentra. But to derive the sexual organs of the first two groups from the last form, it would be necessary to postulate the suppression of two important activities in Vaucheria, namely, the development of motile sperms and the formation of pores in the gametangia for the entrance and exit of these structures. The suppression of the pore formation and consequent modification of the sexual cells, the establishment of several coenocentra in the Saprolegniales, and the specialization of a periplasm in the Peronosporales are peculiarities involving very important protoplasmic activities not represented in Vaucheria.

We have in the Saprolegniales and Peronosporales the interesting association of complex female organs developing eggs, with male organs that are much simpler. The antheridia in the first two groups are all mutinucleate and morphologically gametangia. In certain forms (*Albugo Bliti* and *A. Portulacae*) the antheridia are actually coenogametes as truly as those of the Mucorales, because large numbers of functional gamete nuclei are discharged into a multinucleate egg. Uninucleate gametes, probably motile in ancestral types, have been given up, and the antheridium, acting as a unit, follows the chemotactic tendencies of a male sexual cell in its fusion

with the female. All of these antheridia behave in the same manner whether there are one or many functional gamete nuclei. This condition must have been closely associated in its origin with the suppression of the habit of forming pores for the discharge of zoospores or motile gametes.

We do not know enough about the pore-forming activity in zoosporangia and gametangia to understand how readily it may be given up, and whether its presence or absence is of great morphological importance. The activity is absent in the gametangia of the Mucorales, Saprolegniales, and Peronosporales, but present in the sporangia of the Saprolegniales and most Peronosporales (conidia which produce zoospores), although lacking in some forms (Peronospora and certain species of Pythium) whose conidia germinate by a tube. The sporangia of the molds may have at one time developed zoospores, but there is at present no hint of such possible activities, except a general agreement in the processes of protoplasmic cleavage by furrows with spore-formation in such zoosporangia as have been studied (Hydrodictyon, Saprolegia, etc.).

If the suppression of the pore-forming activity may take place readily after some slight change in life-habits, there would seem to be no great difficulty in relating the processes of oogenesis in Saprolegnia and the Peronosporales rather closely to Vaucheria or relatives of Vaucheria. But if pore-formation may be given up only under exceptional conditions and infrequently, then it becomes very questionable whether there can be a close relation to Vaucheria, and we must look to another line of ancestry for the Saprolegniales and Peronosporales. The author thinks the latter condition at least quite possible and deserving of further consideration.

Such an ancestry for the Saprolegniales and Peronosporales would naturally be sought through simpler conditions, somewhat like those illustrated in the Mucorales whose gametangia are coenogametes. It is scarcely conceivable that the molds are very closely related to the first two groups, but their coenogametes illustrate such well-defined sexual conditions that they naturally enter into the discussion. It is possible that groups with coenogametes like those of the molds might gradually differentiate such structures until they would finally become male and female sexual organs. The female

coenogamete would be larger and well supplied with food material, and might finally develop one or more eggs and thus become an oogonium; the male coenogamete in contrast would remain small or perhaps become further reduced and would be called an antheridium when it bore a sexual relation to an oogonium. Thus conditions like these of the Saprolegniales and Peronosporales might arise from coenogametes resembling those of the molds, and a condition of heterogamy result, which would closely resemble that of Vaucheria and yet have no genetic relation to the latter condition. The eggs of the Saprolegniales and Peronosporales in such an event would have an origin entirely independent of any other line of sexual evolution, and with the conspicuous peculiarity of coenocentra marking the position of dynamic centers during the process of oogenesis.

A question sure to be raised in this connection is the possibility of undifferentiated coenogametes of the mold type arising through the simplification or degeneration of organs like the antheridia and oogonia of the Saprolegniales and Peronosporales. Such a line of evolution would demand the suppression of some very highly differentiated cell processes, such as the extensive nuclear degeneration, the formation of coenocentra, and the differentiation of periplasm. There is no evidence of such tendencies among the forms in question, but, on the contrary, excellent reasons for believing that the direction of sexual evolution is toward greater and more precise protoplasmic complexity rather than simplification. The point is especially well illustrated in the series of species in the genus Albugo, where the line is clearly from the multinucleate egg and small coenocentrum of *A. Bliti* to the uninucleate egg and extraordinary large coenocentra of *A. candida* and *A. Lepigoni*. The author can see at present no probability of a line of sexual degeneration or simplification from higher forms toward the molds.

For these reasons we are driven to consider the possibility of an origin of the coenogametes of molds from gametangia that have not passed the stage of isogamy. I have previously (DAVIS '00, p. 308, and '03, p. 335) advanced the hypothesis that such coenogametes may have arisen from gametangia somewhat like those now found among the lower Siphonales and in Cladophora. These gametangia are generally terminal structures that discharge motile gametes.

But should organisms of this type (whether algae or fungi) be placed under conditions unfavorable for the formation of motile gametes, the gametangia themselves might be expected to act as coenocytic units, and obeying the chemotactic influences of sexual cells fuse with one another as coenogametes.

So the problems of phylogeny in this higher region of the Phycomycetes become greatly complicated through factors that concern the environment and life-habits of the forms in question. The absence of pores in structures that at one time evidently formed motile gametes presents great difficulties to the establishment of relationships between the Mucorales, Saprolegniales, Peronosporales, and Vaucheria. Yet, it may be that the suppression of this structure indicates little more than a change in life-habit from an aquatic to an aerial existience (Mucorales) or to a parasitic life (Peronosporales), with the apogamous Saprolegniales presenting conditions peculiar to themselves. But until we know more about these life-habits and the possibility of an organism passing from one condition into another, it is pure speculation to lay out lines of relationship. And again, we lack knowledge of the processes of oogenesis in a number of forms which may have important bearings on these problems of phylogeny (especially for Monoblepharis and Sphaeroplea).

In spite of the complications of the problems of phylogeny in the Phycomycetes, certain features stand out clearly which may be briefly summarized. The multinucleate character of the sexual organs in types of the Mucorales, Saprolegniales, and Peronosporales thus far studied, and perhaps some other forms as well (Monoblepharis) is likely to prove universal in these groups. Numerical reduction of potential gamete nuclei takes place through degeneration, a process of great physiological interest which deserves careful study. The suppression of the pore-forming activity gives the closed oogonium and antheridium peculiar to the fungal groups. The coenogametes characteristic of the Mucorales and also illustrated by certain of the Peronosporales (*Albugo Bliti, A. Portulacae*) are morphologically gametangia and probably have had their origin by the suppression of the processes of cleavage to form many gametes and their assumption as coenocytic units of sexual attributes. The Saprolegniales and Peronosporales exhibit the further peculiarity of

eggs differentiated around dynamic centers (coenocentra), with the specialization of a periplasm in some forms. Perhaps the highest expression of periplasmic development is the cellular envelope which finally invests the egg of Araiospora.

## SUMMARY OF THE INVESTIGATION OF VAUCHERIA.

The oogonium arises as a process containing dense protoplasm with many plastids and nuclei. As the young structure increases in size, vacuoles develop in the protoplasm, which consequently forms a peripheral layer next the cell wall.

The number of nuclei is variable, but always large, probably ranging from 20 to 50. There are no mitoses in the oogonium.

The oogonium becomes separated from the parent filament by a cross wall which is developed between two plasma membranes that appear to be formed along the surfaces of flattened vacuoles.
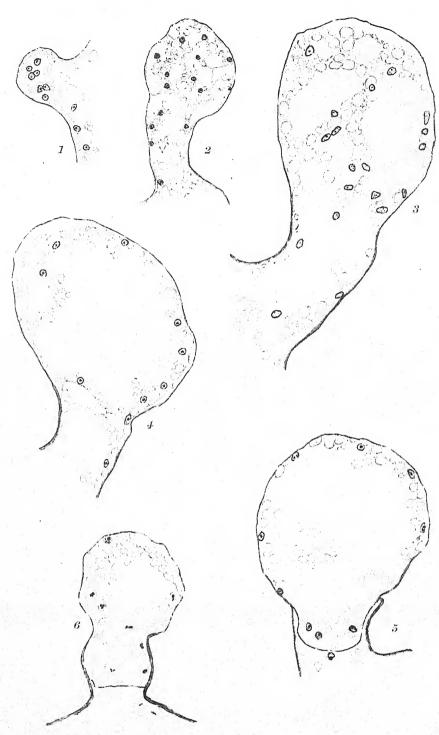
The oogonium is multinucleate at the time the cross wall is formed; but even then there is evidence of the degeneration which becomes much more pronounced later.

In older oogonia the degenerating nuclei are found chiefly in the periplasm. They become exceedingly small, the nuclear membrane disappearing first, and finally nothing remains but granular matter, apparently nucleolar, which is finally lost in the cytoplasm of the cell.

A single nucleus survives the general processes of degeneration. This becomes the gamete nucleus and takes its position near the center of the egg, which is probably the situation most favorable for its growth. There is apparently no coenocentrum in the egg of Vaucheria, but the surviving nucleus frequently lies in a mass of rather dense protoplasm which may readily represent a center of metabolic activity.

There are excellent reasons for believing that all of the nuclei in the young oogonium are potentially gamete nuclei, and that the selected egg nucleus owes its survival and later growth entirely to the good fortune of a favorable situation in the cell.
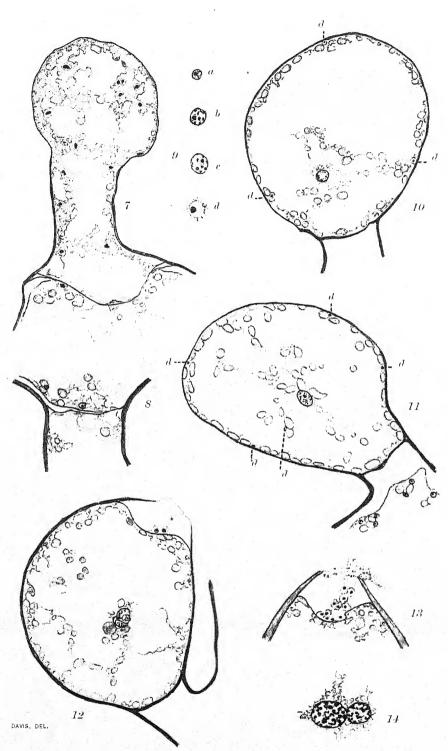
The gamete nucleus grows rapidly until it is finally three or four times the size of the nuclei in the young oogonium. There is a marked increase in the amount of chromatin, which fills the interior
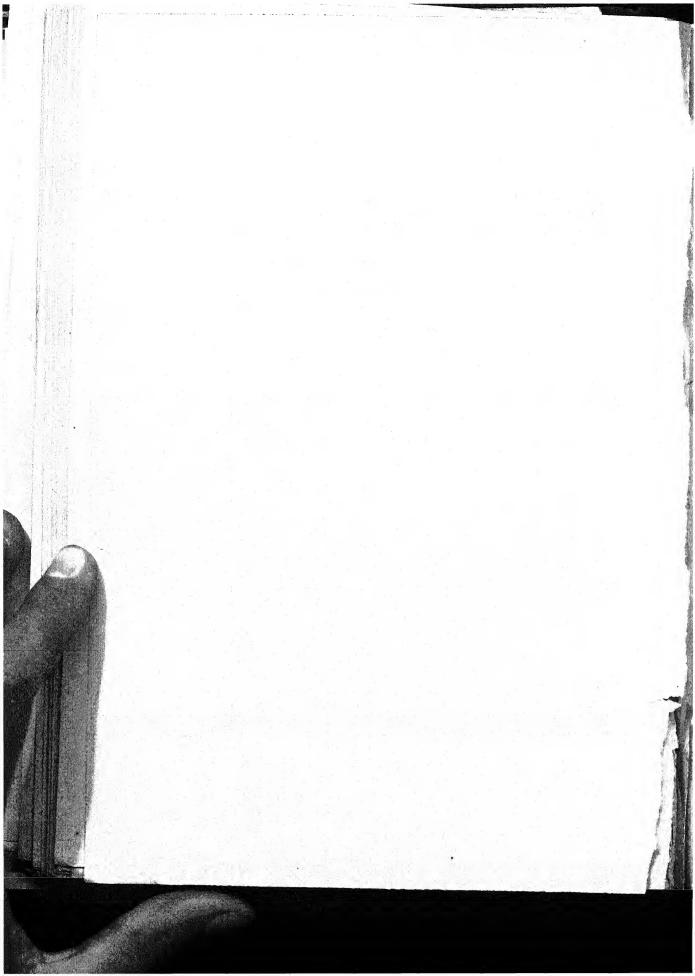
*1*

*2*

*3*

*4*

*5*

*6*

DAVIS, DEL.

DAVIS on VAUCHERIA.

DAVIS, DEL.

DAVIS on VAUCHERIA.

of the nucleus with numerous small granules on a delicate linin network.

After fertilization the nucleus of the sperm passes to the center of the egg, where it increases in size at the side of the female nucleus in the same region of dense protoplasm. The two sexual nuclei fuse slowly when both are approximately of the same size.

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## EXPLANATION OF PLATES VI AND VII.

The sections were cut $5\mu$ thick and stained with safranin and gentian violet. All figures were sketched with an Abbé camera under the Zeiss apochromatic objectives $2^{mm}$ or $1.5^{mm}$ in combination with compensation oculars. The magnification is as follows: *figs. 1-2*, $\times 500$; *figs. 3-8* and *10-13*, $\times 667$; *fig. 9*, $\times 2,000$; *fig. 14*, $\times 1,334$.

Fig. 1. Oogonium beginning to develop.

Fig. 2. Young oogonium.

Fig. 3. Young oogonium, large vacuoles forming.

Fig. 4. Oogonium, flattened vacuoles marking the positions where the cross wall would have been formed.

Fig. 5. Oogonium, delicate cross wall just formed.

Fig. 6. Oogonium, delicate cross wall, nuclei showing signs of degeneration.

Fig. 7. Oogonium, cross wall, nuclei degenerating.

Fig. 8. Cross wall between two plasma membranes.

Fig. 9. A series of nuclei from the same section to illustrate the process of degeneration with the gradual disappearance of the chromatin and the fading of the nuclear membrane: *a*, from antheridium; *b*, from just below the antheridium; *c*, from near the oogonium; *d*, from within the oogonium.

Fig. 10. Old oogonium with gamete nucleus in the central mass of protoplasm and degenerating nuclei (*d*) in the peripheral layer.

Fig. 11. Oogonium older than *fig. 10* and probably mature, remains of degenerating nuclei (*d*) in the peripheral layer of protoplasm.

Fig. 12. Fertilized egg, gamete nuclei fusing in a mass of dense protoplasm.

Fig. 13. Tip of oogonium showing mass of sperms in the slime at the opening.

Fig. 14. Gamete nuclei showing comparative size and general similarity in structure when about to fuse.

# A STUDY OF TILLANDSIA USNEOIDES.

Frederick H. Billings.

## (WITH ONE FIGURE AND PLATES VIII–XI)

*Tillandsia usneoides*, popularly called "long moss," "black moss," or "Spanish moss," is the most widely distributed representative of the tropical and subtropical family Bromeliaceae. According to Schimper (1) it extends from southern Virginia, its northern limit, as far southward as the Argentine Confederation. It forms everywhere a conspicuous and characteristic object of the landscape, its long gray festoons adorning not only trees of the virgin forest but many cultivated ones as well. Although the beauty of the landscape is enhanced by its presence, its growth upon ornamental trees is regarded often with apprehension, a common impression being that it lives parasitically. A most casual examination, however, will reveal the fact that the moss is in no way connected with the tree, but merely wraps its dead, wiry stems loosely around the twigs in order to support itself. Old festoons which have hung in the same place for years occasionally show a connection with the bark, the annual growths of the limb finally enclosing some of the decorticated moss stems; much in the same way that an old horseshoe hung astride a branch and left unmoved for a long time will be partially enclosed.

An indirect cause of the popular belief in the parasitism of Tillandsia is its preference for sunny exposures. This habit would tend to keep it from trees having a dense shade. In dark forests it hangs suspended from the higher limbs of tall trees, especially those that are dead. Many a cultivated tree when in perfectly healthy condition possesses too dense foliage to serve as a host for Tillandsia, but if for some reason the supply of leaves should be reduced, the light conditions might be such as to make the presence of the epiphyte possible. Should it make its appearance, the owner of the tree would be very apt to regard the moss as the cause rather than the result of the reduced foliage. A proof of the true epiphytism of the plant is its long-continued and vigorous growth upon decorticated limbs of dead trees. Near Baton Rouge are many such trees, killed by girdling long ago,

yet supporting a large quantity of moss. In order to demonstrate experimentally that the moss can live solely on what it derives from air and rain, some festoons were supported by twine and hung from some branches of a tree upon which moss was already growing. As was expected, the festoons produced normal flowers, gave rise to new growth, and at the end of eighteen months looked as vigorous as any on the tree, though they came at no time in contact with it.

Because Tillandsia has no influence as a parasite, it does not follow that it exerts none in other ways, yet to just what extent it affects a host tree is at present difficult to say. Aside from the slight damage done in breaking twigs and small branches by its weight, it is doubtful whether such objections as shading and cutting off the supply of air are really worthy of consideration. It is almost certain that these objections are not sufficient to explain a reduction in foliage that people so often ascribe to the presence of the moss. It is realized, however, that this problem can only be answered satisfactorily by experiments extending over a considerable number of years.

The problem of the distribution of *T. usneoides* upon the various species of trees is one of the first to force itself upon the observation. That certain trees of a given locality are abundantly supplied while others not far distant are not, is a well-known fact. One factor in the case has already been mentioned, and that is the light relation. But there are others to be considered, and the most important perhaps is concerned with the method of dissemination. The epiphyte is not usually propagated by seeds but by fragments of festoons, which being somewhat heavy cannot be carried far except in a very high wind, or by birds, which according to SCHIMPER (1) in some regions utilize the plant in building their nests. There is a good chance, therefore, for a tree a little distant from others bearing the moss not to receive its first detachment of the epiphyte.

The character of the foliage also plays a part, in that a tree with leaves densely crowded on the outermost twigs would scarcely permit a wind-blown fragment of moss to hook itself to the branches, but would shed it. SCHIMPER (1) observes in this connection that "Bäume mit sehr dichtem Haube entbehren der Sonnenepiphyten beinahe gänzlich." According to PEIRCE (2) *Ramalina reticulata*, a lichen having a habit and mode of dissemination similar to *T. usneoides*,

is found more frequently on deciduous than on evergreen trees, because, as he explains, the foliage of the evergreen trees interferes with its reaching the branches. The umbrella tree (*Melia Azederach*) has a remarkably dense foliage and is almost universally devoid of moss, yet near the university is a tree of this species with a scanty supply of foliage and an abundance of moss. It is reasonable to conclude that any tree furnishing proper conditions for attachment and growth may become a host of the epiphyte.

The source of the water supply of Tillandsia is atmospheric precipitation, as in all epiphytes. Dissolved in the water are the necessary salts which have been dissolved by the rain from the dust in the air. Perhaps an equally fruitful source of salts is in many cases the washings from the tree, which in dry weather may accumulate much earthy material in the form of dust upon its branches. The plant itself even serves in collecting dust on account of the scaly surface, so that when wet the deposits beneath the scales yield a small amount of soluble material.

A most remarkable characteristic of Tillandsia is its ability to retain water. The absorption of water is accomplished over the entire surface of the living parts by means of scales, as will be described further on, its retention being accomplished also by the scales, and of course by the cuticularized epidermis. It is much easier to understand how a melon cactus with its globose form and consequent minimum surface and enormously developed water-storage tissue can resist prolonged drouth than it is to see how Tillandsia with its small cylindrical leaves, much greater surface exposure, and comparatively small storage facility can, without any water supply, endure drouth. A small festoon was hung in a closed dry room for nineteen days without water. It lost 23 per cent. in weight during the time, but when placed in water it absorbed as much as it had lost, and remained a healthy plant, showing that it had not really suffered injury by exposure to the drouth. There is occasionally, of course, a similar drying process in the open air when drouth occurs. During the dry spell in the spring of 1902, moss plants were known to have been subjected to two months of rainless exposure without injury.

From an economic standpoint, Tillandsia is of some commercial value on account of its mechanical tissue. This forms a central

cylindrical strand composed of reduced phloem and xylem, surrounded by a mass of thick-walled sclerenchyma fibers. When the parenchymatous cortex is removed, the sclerenchymatous axis remains as a tough elastic fiber, which serves as a packing in upholstery. The so-called curing process is a means of eliminating the parenchyma. One method largely employed is that of burying the moss in trenches or pits, allowing it to remain till the cortex is dead and in a condition to be removed easily.

### DEVELOPMENT OF THE EMBRYO SAC.

The primordia of the ovules arise on the innermost wall of each loculus of the tricarpellate, superior ovary. By a one-sided growth each primordium becomes bent toward the base of the ovary, developing into the anatropous type of ovule. When the bending has reached an angle of about 90°, the nucellus appears as a hemispherical mass of cells, at the base of which can be seen the beginning of the inner integument. Imbedded under two layers of nucellus cells, the single archesporial cell becomes differentiated in the usual way, by its slightly larger size and greater staining capacity (*fig. 2*). As the ovule increases in size, the nucellus elongates, the outer integument appears, and the archesporial cell enlarges considerably, especially in length. There is no parietal cell formed, but by multiplication of cells the nucellus over the archesporial cell forms an additional layer, making three (*fig. 3*). The archesporial cell is now much elongated, and occupies the central region of the nucellus. It is filled with granular, longitudinally-striated cytoplasm, and has a relatively large nucleus. The first and second divisions of this nucleus probably give rise to the gametophyte generation. Only one spindle of the first division was observed, and it was but little more than one-third the length of the cell (*fig. 4*). The chromosomes were short, and closely crowded at the equatorial plate. The conditions were altogether unfavorable for ascertaining their number on account of the small size of the figure. The number, however, was definitely made out from the second division of the pollen mother cells, and was found to be sixteen. A protracted search failed to yield a nuclear figure which definitely showed the chromosome number in the sporophyte, though considerably over sixteen were observed.

The first division of the archesporial cell is usually followed by a transverse wall and a resting condition of the nuclei (*fig. 5*); but a single case was observed, as reported by SMITH (3) for *Eichhornia crassipes*, in which a row of four nuclei was formed without separating walls (*fig. 7*). In Eichhornia the absence of the walls is said to be the rule, but in Tillandsia it is the exception. The division which gives rise to the third and fourth megaspores, thus completing the axial row, will be seen from *fig. 6* to be in the cell nearest the micropyle. In the meantime, the basal of the two proximal megaspores begins to elongate, and is destined to develop into the embryo sac. A vacuole is formed in this cell as it pushes outwards crushing the other three megaspores, whose contents soon show evidence of breaking down. The remaining stages in development are the familiar ones of complete absorption of the non-functional megaspores by the functional, and the internal division of the latter into eight cells. The two cells that are to form the synergids soon come to possess larger nuclei than does the egg cell. The egg nucleus in fact is smaller than is customarily observed. In the completed embryo sac, the egg often lies against the wall of the sac near one synergid, but may occupy a position between the synergids. The polar nuclei usually approach each other and fuse near the antipodal region (*fig. 14*). The antipodals occupy a pocket at the extreme end of the sac.

<div align="center">FERTILIZATION.</div>

The pollen tube passes through the micropyle, penetrates the nucellus, and enlarges as it enters the embryo sac. It does not appear to pass between the synergids, but to one side of them, one synergid being disorganized in the process. The two male nuclei which have arisen from the generative nucleus during the development of the pollen tube lie near together and a little in advance of the tube nucleus. In no case observed did the male nuclei show the much elongated, spermatozoid-like form so often described for other plants. In *fig. 15*, which represents the tube before its rupture, they are elliptical; but when discharged they are slightly more elongated and may have pointed ends. The place of discharge may be either at the end of the tube or lateral, though near the end (*figs. 16–19*). The tube nucleus is usually to be seen at the time of dis-

charge of the male nuclei, but may be absent later, which would indicate that it too was ejected. In one instance (*fig. 19*) the nucleus was observed after ejectment. The male nuclei are of about the same size and appearance, and leave the pollen tube at about the same time. The nucleus which is to fuse with the endosperm nucleus can be seen in various stages of its passage to the antipodal end of the embryo sac. There is no evidence that either nucleus increases in size after leaving the pollen tube. The time of fusion with the polars may be either before or after their complete union with each other; in *fig. 18* it is before. In *fig. 18* the fusion of the two male nuclei with the egg and polar nuclei respectively is seen to be simultaneous. After fertilization the egg secretes a wall about itself and rests for a time.

The occurrence of darkly-stained bodies so frequently seen in pollen tubes has been noted in Tillandsia. They were observed in the microspores before germination, which would account for their presence in the pollen tube.

### THE SEED.

The most noticeable change that results from fertilization is the extensive elongation of the entire ovule. Part of the growth is due to enlargement of the embryo sac and its surrounding integuments, while the remainder is traceable to elongation of that part of the outer integument which is prolonged above the body of the ovule. The inner integument does not appear to elongate at all, hence the opening of the micropylar canal comes to lie far below the opening of the canal formed by the outer integument (*fig. 22*). A similar elongation of the outer integument was observed in *Puya chilensis* by HOFMEISTER (4).

Accompanying the growth of the embryo sac is the development of the endosperm. It begins to form at once after fertilization, and the nuclei resulting from the first divisions of the endosperm nucleus take position at either end of the sac, leaving, however, a few to form a thin parietal layer between. At the antipodal end, cell formation with walls begins at once, and a number of large cells form a tissue which stands out conspicuously in the cavity of the sac, which otherwise contains only a few free endosperm nuclei. At first this tissue

was taken as an extraordinary development of antipodals, but cases
were found where the three degenerate cells were lying beneath the
tissue in the small pocket at the end of the embryo sac. The free
endosperm nuclei gradually gather in increasing numbers against
the endosperm tissue, finally forming walls about themselves but
remaining readily distinguishable from the other tissue (*fig. 24*).
The functions of the two tissues appear to be somewhat different.
The originally formed cell-compact retains its richness of protoplasmic
contents during the development of the embryo, probably serving
in the conduction of food materials to the later formed tissue adjoining
it, which soon shows signs of containing food deposits. The reserve
materials thus laid down are not utilized by the embryo before seed
germination, but exist as the endosperm of the ripe seed. The endo-
sperm at the micropylar end of the embryo sac does not develop in
large quantity, forming a tissue about the embryo only after the
latter attains a considerable size.

The egg cell remains dormant for a· time after fertilization. In
1903 the period of blossoming lasted (at Baton Rouge) for a month
following the middle of May. Material gathered about the first
of July showed egg cells undivided, as well as embryos of only a few
cells. Growth during the summer is slow, small embryos being
found in material gathered about the tenth of August. It was not
till the middle of September that large ones were observed, and even
then there was much diversity in size.

The first wall formed in the division of the egg cell is transverse,
as is the second one also. The proembryo of three superimposed
cells is therefore not different from the type that holds in so many
monocotyledons. The divisions immediately following, however,
vary considerably in sequence.

The middle segment may divide sooner than the terminal (*fig.
28*), or the reverse may be true (*fig. 27*). The basal segment divides
sooner or later by longitudinal walls into four cells—a variation from
the Alisma-type, in which the segment is unicellular and vesicular.
The terminal segment divides by longitudinal walls to form the
quadrant, and by transverse walls to form the octant. The latter
walls instead of being precisely transverse may be oblique (*fig. 34*).
In many older embryos the arrangement of the cells in this segment

indicates that the walls in question were originally oblique or else became so by unequal growth in different parts of the embryo (*fig. 36*). The dermatogen usually forms first in the terminal segment. To distinguish the middle from the terminal segment soon becomes a difficult matter, but from the position of the concavity in which the stem apex is developed, it is safe to say that the apex arises from the middle and the cotyledon from the terminal segment, as in Alisma. The middle segment also gives rise to the root-tip, hypocotyl, and part of the suspensor. A short time before the differentiation of the stem tip in the lateral depression, the region adjoining and outside of the area where the stem tip is to appear grows upward into a ridge of tissue, which in the mature embryo encloses the growing point completely. If the figure of the embryo of Guzmannia, as shown by WITTMACK in Engler and Prantl's *Natürlichen Pflanzenfamilien* be compared with that of *T. usneoides* (*fig. 40*), the resemblance will at once be apparent. It will be noticed that what I have called cotyledon in Tillandsia is called scutellum in Guzmannia, the term cotyledon[1] being reserved by WITTMACK for the small outgrowth labeled *c*, near the stem apex. It is probable that the author in thus naming the two organs scutellum and cotyledon only wished to emphasize the difference in function, one as an organ of absorption, the other as a rudimentary leaf, at the same time recognizing the two as homologous with the cotyledons of the dicotyledons. From a study of the seed germination of *T. usneoides*, however, it will be seen that it is extremely doubtful if the organ named cotyledon in Guzmannia is really such. Further discussion of this point, however, will be postponed till seed germination is considered.

When the embryo of Tillandsia is about three-fourths grown, there occurs a degradation of certain cortical cells of either the root or the end of the hypocotyl nearest the root-tip. The cells in question show at first a contracted protoplast, with incapacity to stain deeply, and by the time the embryo has reached its full size almost a complete absence of cell contents (*fig. 42*). This phenomenon undoubtedly stands in intimate relation with the complete atrophy of root that obtains in the mature plant.

[1]The index letter *c* in the description of *fig. 19, G* of the Bromeliaceae has been found through correspondence to indicate cotyledon.

Dispersal of seeds in the Tillandsia is accomplished by the assistance of long delicate hairs that beset the seed coat. These arise by elongation of the cells of that part of the outer integument which forms a portion of the body of the seed, and also from that part which extends to the funiculus. The hairs not only assist in wind transportation, but are also of use to the seed in enabling it to adhere to bark or festoons of moss. The adaptation for effective adherence consists in closely appressed barbs attached to the hairs at intervals (*fig. 44*). Soon after the opening of the capsules, numerous instances of seeds clinging tightly to limbs and to moss festoons may be observed.

The time of discharge of seeds is in March (at Baton Rouge). I have no data as to possible variation of this time in localities widely distant, but suppose it is nearly uniform for the southern states. March, of course, is an unusual month for dehiscence of fruits in the north temperate zone, but in Tillandsia it stands in close relation to another property not generally possessed by seeds in temperate climates, that is, quick germination. Though lack of facts forbids positive statement, it may be conjectured that this relationship originated from ancestors living in tropical lowlands, where a dormant period to withstand unfavorable conditions is unnecessary.

### GERMINATION OF THE SEED.

Tillandsia produces seed in considerable quantity each year. Just what proportion contains fully-matured embryos has not been ascertained, but there is no doubt that a large percentage have them. The embryos appear perfectly normal, with the exception of the dead cortical cells in the root or hypocytl, and show no apparent reason why they should not give rise to seedlings. The experience of investigators, however, has been that seeds produced by the epiphyte are worthless, a condition which has arisen through the introduction of a vegetative mode of reproduction, whereby seed-production has degenerated. Nevertheless, I made efforts to induce seeds to germinate by placing them in a germinator, but without success. MEEHAN (5) reports having found the seed germinating in the hollow crotch of a tree in which vegetable mold had collected. He says that from the seedlings or young plants proceed stolons or runners, having buds

every few inches, which push out into leaves and stems to form the gray-green moss. SCHIMPER (1) succeeded in finding one seedling, but he gives no description of it. MEZ (6) states he was unable to obtain any seedling at all. Realizing that the observations of MEEHAN were worth consideration, I searched crotches of moss-laden trees, in which plenty of vegetable mold had collected, but without success.
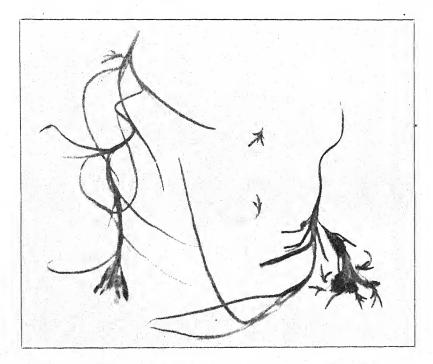


FIG. 1.—Seedlings of *Tillandsia usneoides;* on the right is a cluster of seedlings still attached by their coma to a partially opened capsule; near the top of the shoot on the left a seedling is adhering to the scaly surface.

I then planted seeds in the mold, but they could not be induced to germinate. On April 6, 1903, I observed Tillandsia seedlings for the first time, and they were projecting from a partially-opened capsule (*fig. 1*). Out of the nineteen seeds in the capsule, thirteen had developed into seedlings. They were held in place by the tuft of hairs from the testa to which they still adhered. An examination of moss festoons was then made, with the result that many little

seedlings were found either still attached to the capsules, or else hanging to the scaly stems and leaves of the mother plants. In every case the seed coat still adhered to the base, or root-end of the seedlings, so as to enable the coma to keep them from falling to the ground, which they certainly would have done without this provision. When it is remembered that the capsules dehisced in March, and the seedlings were found early in April, it will be seen that germination followed dehiscence quite closely. Of course the early growth was attained at the expense of the endosperm, but when it was exhausted, continued growth, which would naturally be expected from healthy looking seedlings, failed to occur. Material gathered in the summer and autumn yielded the usual crop of seedlings, but in no case were any found that were larger than those found in April. Festoons gathered the middle of January, nearly a year after the capsules opened, had numerous little seedlings hanging to them, all healthy looking, but no larger than any observed before them. It is expected that when the warm weather of spring comes, when Tillandsia puts forth its most vigorous growth, the seedlings also will increase in size. The question naturally arises here, why Tillandsia seedlings are not to be seen in all stages developing into mature plants, counting of course those which germinated previous years. As such is not the case, it can only be conjectured that, as the spring of 1903 was an unusually rainy one, the conditions for germination were especially favorable.

Seedlings exhibiting various stages in germination were imbedded in paraffin and longitudinally sectioned. In the earliest stage (*fig. 45*) the first leaf shows only a slight growth, the stem apex is still undifferentiated, while from the axil of the ridge of tissue that enclosed the stem apex, or else from its inner surface, a pair of organs have arisen. It is believed that the presence of these organs throws some light upon the morphological nature of the ridge of tissue. If a section is made through the nodal region of a mature plant (*fig. 49*), it will be seen that the leaf sheath which encloses the lateral shoot and main axis is double. The doubling is not due to splitting of a tissue once entire, but to bifurcation. A section through a very young sheath (*fig. 49a*) reveals an outgrowth, one to several cells in extent, from which a double layer of cells arises. These soon separate to

form the double sheath. In older stages the base of the sheath is composed of many cells in width, so that the sheath appears no longer to originate as a bifurcation of a single organ, but rather as two distinct organs. Both organs or portions of the sheath may develop equally, though it more often happens that one portion becomes larger than the other. Occasionally, the inner scarcely develops at all, but remains a tiny rudiment.

The sheaths which arise in the seedling develop precisely like those in the mature plant and differ from them in no respect. The two organs that originate on the ridge of tissue, therefore, may be regarded without hesitation as the first sheath, and as every sheath appears in connection with a leaf, that leaf must be the cotyledon. From the section of the mature plant it will be noticed that the bases of each leaf and its sheath are at the same level on the axis. If a difference in level should occur, however, whereby the base of the sheath were elevated above that of the corresponding leaf, the cell growth producing that elevation would originate from the cortical parenchyma lying immediately under the sheath. The parenchyma would give rise to a ridge bearing the sheath upon its summit. Such an occurrence does not of course actually take place in the mature plant, but it is believed that it is in such a way that the ridge of tissue originates in the embryo. Reasons for coming to this conclusion are based upon the position of the first sheath. While the inner portion of the sheath may grow from the crotch at the base of the ridge of tissue, the outer, and sometimes the inner also, is attached to the ridge upon its inner surface. The outer portion may in fact arise from the summit of the ridge. The base of the sheath, therefore, is on the whole raised above that of the cotyledon, the elevation being accomplished through growth of the subjacent parenchyma. Thus there develops a special organ which serves a special purpose, perhaps as protection to the stem apex, and which must therefore be regarded as an embryonic structure without an exact counterpart in the adult plant. It cannot be a leaf, or a cotyledon, because a leaf does not bear such a relation to its sheath. A leaf and its sheath always develop with a growing point between them, so that they can never join in a median section. CAMPBELL (7) calls a similarly placed though less extensive outgrowth in the embryo of Sparganium a sheath. While it does not require a

stretch of the imagination to consider the growth in question a sheath, there is at least one objection to this solution of the problem. The development of the sheath shows that it appears as a bifurcated organ almost from its incipiency, and that the base, at first narrow, subsequently increases greatly in width. Quite the reverse would be true in the embryo if the organ enclosing the growing point were regarded as a sheath, for the basal portion is first enormously developed, leaving the upper bifurcated portion to appear comparatively late.

The stages in germination are shown in *figs. 45–48,* which should be compared with *fig. 49.* The latter exhibits a difference in relative time of differentiation of stem and leaf apex as compared with the seedling. In the mature plant the leaf is still quite small when the stem apex becomes distinguishable at its base, while in the seedling the leaf first attains considerable size.

### THE FLOWER.

The flowers, which are produced in considerable quantity in May and June, present little of special interest. Each flower has a calyx of three sepals, and a corolla of three green petals. Having a fragrant odor, it is possible that it is visited by insects, though no information has been collected by me on the subject. Thrips, however, inhabit many of the flowers and puncture the style in order to deposit an egg at its base. It is possible, therefore, that they may serve in cross pollination.

Although the flower appears to be terminal, it is regarded by Mez (**6**) as a reduced indeterminate inflorescence. An examination of preparations made longitudinally through buds bears him out in his statement, for a growing point of considerable size is present, though having dead meristem tissue.

### THE LEAVES.

The leaves of *T. usneoides* are acicular and with an approximately semicircular cross section. The epidermal cells do not have specially heavy walls, nor are the inner ones thicker than the outer, as in certain other Bromeliaceae. Sections through the leaf show it to have three fibrovascular bundles, each surrounded by a tissue composed of thick-walled sclerenchyma fibers (*figs. 50, 51*). The principal portion

of the leaf is composed of parenchyma cells which do not show any differentiatiation at all into palisade and spongy tissue. While the cells have the shape of those in typical spongy tissue, the large intercellular air spaces characteristic of most mesophytic leaves are here replaced by small ones, giving the whole tissue a much more compact appearance. Not all of the parenchyma cells contain chloroplasts, for there are interspersed cells without them, whose function is that of water-storage, having walls provided with large pits which facilitate the passage of water from one cell to another.

Aside from acting in the capacity of mechanical tissue, the vascular system has undergone a process of degeneration. The necessity for a functional xylem with its transpiration stream is eliminated by the fact that there is a complete absence of roots, and also by the fact that the water-absorbing organs, the scales, are found over the entire exposed surface with the exception of some of the floral organs. There would appear also to be no need for a functional phloem since all living cells either contain chlorophyll and are exposed to light, or else are approximate to those containing chlorophyll.

### THE CHLOROPLASTS.

One of the most interesting features of the leaf is the structure and behavior of the chloroplasts. These bodies, instead of exhibiting the more or less homogeneous structure observed in most chloroplasts, are seen to be composed of masses of smaller chloroplasts, measuring about $2\mu$ long and about a third as wide (*fig. 52*). While a very few cells in every cross section of the living leaf contain chloroplasts of the usual type, the vast majority of them contain such as have been described above. The little chlorophyll bodies have almost, if not quite, the minuteness of bacteria, and for convenience will be spoken of as *microchloroplasts;* the larger bodies, of which they appear to form a part, being distinguished as *megachloroplasts*. The true significance of the formation of the microchloroplasts will be readily seen when it is stated that they may not remain in bunches (*fig. 52*), but can and often do separate from one another till the entire cytoplasm of the cell becomes dotted with them (*fig. 53*). Under a low magnification such a cell appears uniformly green throughout. They even enter the vacuoles, where a lively Brownian movement is set up.

It was at once suspected that the various phases in distribution of the microchloroplasts were conditioned by the light intensity, and hence their movements could be made subject to control. Festoons of Tillandsia accordingly were placed under different conditions varying from darkness to direct sunlight. Those placed in darkness were allowed to remain there 24 to 30 hours, and a similar period of exposure was allotted to festoons hung in the shade. Those exposed to direct sunlight were hung up early in the morning. All were examined during the hours between 11:30 A. M. and 3:00 P. M.

The examination was made by sectioning numerous leaves of various ages, and from as many different regions of each festoon as possible. Plants were also sectioned at different times of day and also at night. The results in every instance were approximately the same. Sections were obtained from plants under the varying conditions of light intensity used in the experiment; sections in which the megachloroplasts were present; in which they were in the process of disintegration into microchloroplasts; in which there was distribution of the microchloroplasts uniformly through the cell; and in which all the foregoing stages were present in the same section. In fact, the same leaf varied in these respects in its different portions. There seemed to be no method of telling before examination just what condition the chloroplasts would be in. One of the best instances of complete uniformity of distribution of the microchloroplasts throughout the cytoplasm was obtained from the tiny leaf of a seedling. That the disintegration of the mega- into microchloroplasts is not the result of injury due to sectioning may be proven by an examination of the entire leaf through the epidermis. Sections also cut thick contain in their centers cells untouched by the razor.

Homogeneous chloroplasts of the usual type were found which showed evidence of undergoing division. Megachloroplasts, in which the microchloroplasts were distinctly visible, were also found showing a deep constriction as though they too were undergoing fission.

Owing to the difficulty of observing well the interior of the leaf through the overlapping scales, it was not ascertained whether the microchloroplasts return to form megachloroplasts or not; but if so it seems certain that the latter would not be constructed of identically the same microchloroplasts a second time.

It is offered in explanation of this interesting condition of affairs that the supply of light of Tillandsia is considerably diminished by the presence of the overlapping scales, which are necessary for water absorption and for protection against too rapid transpiration. In order to meet this diminution, it not only prefers sunny exposures, but has modified its chlorophyll-bearing apparatus by causing it to occupy a much larger area in order to utilize to better advantage such light as penetrates to the interior of the leaf.

It may be stated here that precautions were taken to examine healthy festoons removed directly from moss-laden trees. In some instances these were examined immediately after such removal, lest confinement in the laboratory should in some way induce pathological conditions.

### THE SCALES.

The scales cover the entire living exposed portion of the plant with the exception of the corolla, stamens, ovary, and a portion of the calyx. Each scale develops from a single epidermal cell, the early divisions of which occur while the young leaves and stems are included within the leaf sheath. The first division is transverse (*fig. 55*). The proximal cell thus produced remains undivided, the distal dividing transversely till four cells are produced, of which the lower three form the stalk of the scale (*fig. 57*). The outermost hemispherical cell becomes divided into four cells by two longitudinal walls perpendicular to one another (*figs. 58* and *63*). By periclinal walls a central group of four cells becomes separated from four outer ones (*fig. 64*). The central cells divide no further. The outer ones divide by periclinal walls to form two concentric rows (*fig. 65*). The cells of both rows become eight in number by anticlinal walls, the inner row undergoing no further division, but the outer, by another set of anticlinals, finally has sixteen. A fourth concentric row is then formed by periclinal walls from the outermost sixteen cells. The three inner layers consist of four, eight, and sixteen cells respectively, which numbers remain constant, but the fourth layer undergoes repeated divisions till a large number of cells are produced (*fig. 67*). These last lengthen greatly and form the wing of the scale. The surface view of the mature scale is seen in *fig. 68*, the longitudinal section in *fig. 70*. All of the cells but the stalk cells and the original

basal cells undergo thickening of their walls in certain portions and lose their cell contents.

SCHIMPER (1) was the first to call attention to the water absorptive function of the scales, and his experiments along this line were so complete as to leave little else to be done. That the leaves of Tillandsia can absorb water is easily demonstrated either by wetting them with water and then watching it disappear, or by noting the weight before and after allowing them to remain a short time in water. That the channel of absorption is through the scales is shown by using colored water, which stains the stalk cells. Unlike most similar appendages of the epidermis, the scales do not hinder the leaf from becoming wet, but actually conduct water into the interstices beneath them. When dry, the leaf is of a gray color, due to the air enclosed by the scales, but when wet, the air is replaced by water, and a deep green color results. From an examination of *fig. 70* it will be seen that the outer walls of the scale are thickened. When water is absorbed by the cells with thickened walls, they become turgid, expand below, and raise the wing of the scale well above the epidermis (*fig. 69*). The water absorbed by the outer cells of the scale passes to the stalk cells, which have thin walls and rich protoplasmic contents. Through these it passes through the basal cell to the water-storage cells of the parenchyma. If the plant be soaked in dilute potassium iodid solution for a day, the walls of the stalk, basal, and neighboring parenchyma cells will be stained. It should be noticed that no ordinary type of epidermal cell with its thickened cuticularized wall separates the scale from the parenchyma. The cell that represents the epidermis beneath the scale is the basal cell resulting from the first division of the epidermal cell that gave rise to the scale. The walls of this basal cell are thin and uncuticularized. If a scale whose wing is raised well above the epidermis by the turgescence of its cells be treated with glycerin, the contraction due to loss of turgescence will draw the scale close down against the epidermis. This illustrates the process that takes place when scales become dry from evaporation, as occurs in nature. Such a process cannot but assist the epidermis in checking transpiration, so that the scales may be considered not only as organs of absorption, but as serving to prevent too rapid escape of the water they have been instrumental in bringing into the plant.

The effect of an absorptive system extending over the entire surface has already been mentioned in the reduction of the mechanical and conductive tissues. As such reduction is found mostly in submerged hydrophytes, it will be seen that *T. usneoides* behaves in these respects much like such plants.

The scales stand in connection with the water-storage tissue. The cells of this tissue lie well distributed among the chlorophyll-bearing cells and keep them in a state of turgescence. Even after a plant has lost one-fourth of its weight by transpiration, and the leaves have become grooved by contraction, the chlorophyll-bearing parenchyma is unhurt. It is believed that the leaf shrinkage is due to a partial collapse of the storage tissue upon loss of water, rather than by decrease in turgescence of the green parenchyma. There is no evidence that the plant undergoes desiccation and subsequent revival, as in the case of *Polypodium vulgare*.[1]

### THE STOMATA.

In addition to protection afforded by scales, hairs, and thick-walled epidermal cells, xerophytes sometimes guard against too rapid transpiration by means of the position and structure of the stomata. Sunken stomata, or those vestibuled by an epidermal air space, itself with a narrow opening to the exterior, are all well known. In some xerophytic plants the usual closing of the pore by the guard cells is assisted in its function of checking transpiration by modifications in neighboring parenchymatous or epidermal cells. In *Kingia australis*, for instance, there is, according to TSCHIRCH,[2] a large intercellular space adjoining the stoma, partially filled with coiled cellular

[1] Since this paper went to press, one by MEZ (9) has appeared on the physiology of water absorption in certain species of Tillandsia, among them *T. usneoides*. MEZ corrects SCHIMPER's observations as to the details of the absorptive process, claiming that the empty cells of the scale do not contain air, but are collapsed when the surface of the plant is dry. The thickened part of the scale swells when wet, raising it and causing the lumen to reappear in the collapsed cells. Water passes from exterior capillary spaces into the partial vacuum through thin places in the cell walls, whence, from the filled cells as reservoirs, the water is taken up and passed into the mesophyll by the stalk cells (*Aufnahmezellen*) through the usual process of osmosis. MEZ describes the scale of *T. usneoides* as having only one stalk cell instead of three. While it is true that two of the cells are very thin, their presence can readily be made out in good sections of mature scales and still more readily in sections of young ones.

[2] HABERLANDT, G., Physiologische Pflanzenanatomie. 2d ed. p. 399. 1896.

outgrowths of the parenchyma. The outgrowths do not stop, but merely hinder transpiration. *Xanthorrhoea hastilis* exhibits a similar contrivance. *Camellia japonica* and *Prunus Laurocerasus* have the faculty of filling up the air space as a result of excessive drouth or by death of the guard cells. In such cases tylose-like processes occur which block up all gas interchange. *Pilea elegans* differs from those mentioned above in that certain subjacent parenchyma cells develop thickenings on their exterior walls. One of these finally pushes up against the pore of the stoma and effectually closes it. There is no movement of the parenchyma cell away from the stoma, hence the aperture is permanently closed. From an examination of *figs. 72* and *73* it will be apparent that Tillandsia presents a condition of affairs not widely different from that of Pilea. The principal difference lies in the fact that in Tillandsia the parenchyma cells undergo no thickening: Both longitudinal and cross sections through the leaf show outgrowths from the parenchyma cells lining the sides of the air space. The outgrowths turn upward and either stop up the opening of the stoma or else press directly against the guard cells. It will be seen that the enormously thickened walls of the guard cells preclude a possibility of change in their form. To show this experimentally some plants were placed in water and exposed to direct sunlight for a few hours. The leaves were then sectioned and the guard cells watched with a micrometer while glycerin was run under the cover glass. There was no measurable change. According to MEZ (6) the guard cells have lost the power of functioning, this power having been transferred to certain cells of the subjacent tissue which operate the passive guard cells, thus opening and closing the stoma. There are two cells which come in contact with the guard cell and may therefore be the means of moving it. One is the cell to which it is attached and which extends from the hinge to the inner face of the guard cell. This cell is usually continuous, but may be divided by a cross wall into two cells. Should this cell, which is epidermal, become turgescent, it would tend to raise the guard cell, swinging its free side outwards. Such a movement, however, would close rather than open the pore of the stoma. The hinge is quite thick and may be much thicker than any shown in the figures. If the epidermal cell is divided the division wall would effectually hinder any movement of

the guard cell. From these two considerations it would appear doubtful whether the guard cells move at all in either direction. Of course the glycerin experiment was repeatedly tried, but no motion was discernible. The only other cells which by contact with the guard cells can move them are the parenchyma cells whose processes push against the guard cells on the under side. It was at first thought that the parenchyma cells were operated by variations in turgescence of the epidermal cell, so that regarding the guard cells as immovable the epidermal cell would press downward upon the subjacent parenchyma cell during turgescence, and lower the process, thus unstopping the stoma. Out of a number of such processes only one reaches the center of the stoma, all the others being considered attempts that from necessity have failed. This explanation of the function of the parenchymatous outgrowth is plausible, to say the least, but it has not been experimentally proven by the glycerin test. Numerous instances were investigated carefully, but in not a single case did any of the processes change their position. It is here confessed that no reaction was noticed in any part of the stoma or adjacent tissue in response to the action of glycerin, nor was an instance found in fresh material where the guard cells appeared to be separated. The experimental demonstration of the presence of a mechanism in the stomata, therefore, has not thus far met with success.

Another explanation might be mentioned, in which the processes are to be considered attempts on the part of the plant to close the stomata permanently. It may be that not all the processes actually reach the center of the stoma and close it, so that, granted that a small opening exists between the guard cells, the number of functional stomata would merely be reduced. The total number of stomata per square millimeter was ascertained and found to be relatively small. The estimate was made by counting the number of stomata in each section of serial sections taken from a portion of leaf of known length. For instance, a piece of leaf $3^{mm}$ long contained 52 stomata. Calculating the surface from the circumference of the cross section, there would be 7 per square millimeter, or, in round numbers, 4,300 per square inch.

It must of course be taken into consideration that *sections* of living leaves were used for experiment and not entire ones. If variations in

the pressure of the water-storage tissue exert any influence on the opening and closing of the stomata it is very probable that the injury done to the tissue in sectioning would greatly interfere with the action of the mechanism.

HABERLANDT (8) figures the stoma of *Tillandsia zonata*, which in respect to guard cells, and their supporting cells, resembles that of *T. usneoides*. The guard cells have greatly thickened walls, and a thickened hinge. From Haberlandt's account it is evident that he does not fully comprehend the mechanism. In *T. zonata* no subjacent parenchyma is mentioned as taking part in the opening or closing of the stoma.

### THE STEM.

Aside from the vascular region, the stem differs in no essential particulars from the leaves as to structure. The stem, of course, has the added function of support, so that there is developed between and around the bundles a thick tissue of sclerenchyma fibers (*fig. 74*). The fibers measure about 750$\mu$ in length. They do not impart rigidity, but flexibility and power to resist longitudinal strain. If a fragment of moss is blown from one limb of a tree to another, and succeeds in getting a hold, the cortex of that portion of the stem that passes over the limb dies, and then disintegrates, leaving the sclerenchymatous axis, which holds the plant in place for several and perhaps many years. It is upon the durability and elasticity of this tissue that the economic value of the moss in upholstery depends.

What has already been said in regard to reduction in the function of the xylem and phloem of the leaves could with equal truth be said about the stems. With a superficial absorptive system and no root, the xylem as a conductive system is useless. The pendent habit and method of dissemination are both closely associated with reduction in mechanical tissue, though they are more likely to be the result than the cause of the reduction. The parenchymatous cortex, as in leaves, is supplied with chlorophyll-bearing cells, all of which are exposed to light, so that a tissue like the phloem, to carry elaborated materials to cells distant from the center of photosynthesis, would be unnecessary.
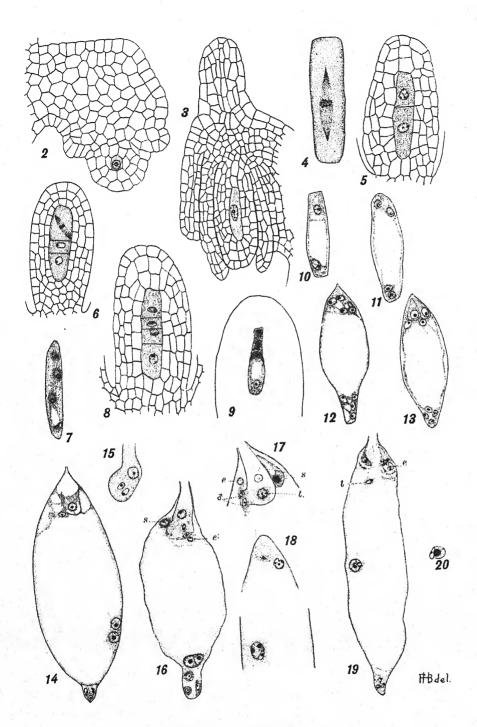
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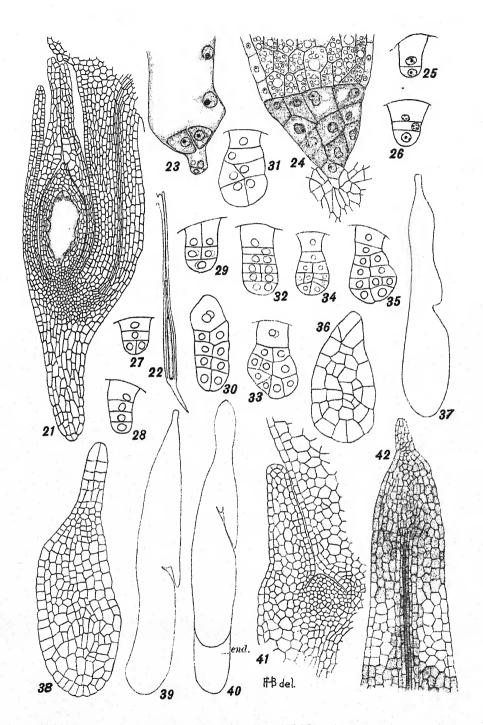
## EXPLANATION OF PLATES VIII–XI.

FIG. 2. Ovule fundament showing archesporial cell.

FIG. 3. Young ovule at period just before first division of archesporial cell.

FIG. 4. Spindle of first division.

FIGS. 5–6. Stages in formation of axial row of potential megaspores.

FIG. 7. Megaspores without separating walls.

FIGS. 8–9. Enlargement of basal megaspore to form embryo sac mother cell.

FIGS. 10–14. Stages in formation of embryo sac.

FIG. 15. Pollen tube just after entering embryo sac.

FIG. 16. Fusion of polars before rupture of pollen tube: *s*, synergid; *e*, egg.

FIG. 17. Lateral discharge of pollen tube: *e*, egg; *t*, tube nucleus; *s*, synergids.

FIG. 18. Simultaneous double fertilization.

FIG. 19. Double fertilization with discharge of tube nucleus (*t*); *e*, egg.

FIG. 20. Fusion of male and endosperm nuclei.

FIG. 21. Ovule at time of completed embryo sac.

FIG. 22. Elongation of ovule and outer integument after fertilization.

FIG. 23. First division in formation of chalazal endosperm tissue.

FIG. 24. Chalazal endosperm tissue and portion of endosperm that is to serve as reserve material in ripe seed.

FIGS. 25–26. Two- and three-celled embryos.
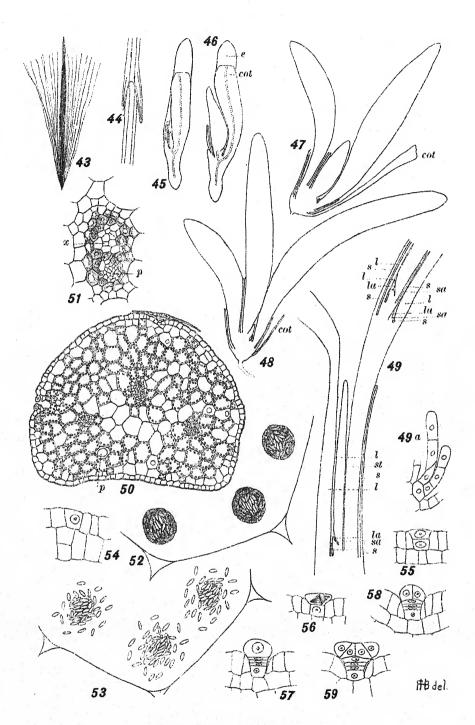
BILLINGS on TILLANDSIA.

BILLINGS on TILLANDSIA.
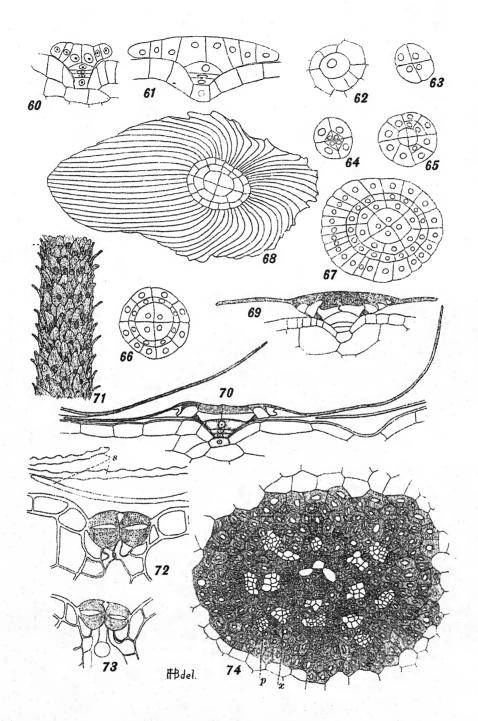
BILLINGS on TILLANDSIA.

FIG. 27.  Formation of quadrant.

FIG. 28.  Division of middle before terminal segment.

FIG. 29.  Unusually early development of basal and middle segments.

FIG. 30.  An unusual form of embryo.

FIGS. 31–36.  Stages in embryo development; in *fig. 34*, the transverse walls in the terminal segment are oblique; the last three figures show beginning of dermatogen.

FIG. 37.  Embryo about one-fourth grown.

FIGS. 38–40.  Outlines of embryos in late stages of development; *fig. 30* represents a mature embryo.

FIG. 41.  Region in vicinity of growing point of a nearly ripe embryo.

FIG. 42.  Root region of nearly mature embryo, showing dead cortical cells.

FIG. 43.  Ripe seed.

FIG. 44.  Barbs on hair of coma.

FIG. 45.  Early stage in germination; outline of longitudinal section.

FIGS. 46–48.  Stages in development of seedling; outline of longitudinal section.

FIG. 49.  Longitudinal section through the growing point regions of a mature plant: *s*, sheath; *st*, stem; *l*, leaf; *sa*, stem apex; *la*, leaf apex.

FIG. 49a.  Very young sheath.

FIG. 50.  Cross section of leaf; *p*, pit in water-storage cell.

FIG. 51.  Bundle of leaf enlarged to show phloem (*p*) and xylem (*x*).

FIG. 52.  Megachloroplasts showing division into microchloroplasts.

FIG. 53.  Stage in separation of microchloroplasts by which they become distributed through the cytoplasm.

FIGS. 54–61.  Stages in development of the scale seen in longitudinal section; *fig. 54* shows the epidermal cell from which the scale arises.

FIGS. 62–68.  Stages in scale development seen from the surface; *fig. 68* shows a mature scale.

FIG. 69.  Scale in longitudinal section, after soaking in water for several hours; the wing is seen to be raised considerably above the epidermis.

FIG. 70.  Scale in longitudinal section, drawn from a paraffin section; it will be seen to lie much closer to the epidermis than the one in *fig. 69.*

FIG. 71.  General appearance of the surface of the leaf, showing the scales.

FIG. 72.  Section through a stoma; the guard cells are unquestionably closed; in addition a process has grown up from the parenchyma into the pore of the stoma; *s*, scales.

FIG. 73.  Section of stoma showing slight variation from that in *fig. 72; figs. 72* and *73* were drawn from sections through living material.

FIG. 74.  Cross section through the vascular region of the stem: *p*, phloem; *x*, xylem.

# BIOLOGICAL RELATIONS OF CERTAIN DESERT SHRUBS.

## I. THE CREOSOTE BUSH (COVILLEA TRIDENTATA) IN ITS RELATION TO WATER SUPPLY.

### V. M. SPALDING.

### (WITH SEVEN FIGURES)

THE general features of desert vegetation are well known and have been described in a voluminous literature. Certain striking peculiarities, such as the production of spines, development of tissue for water storage, and particularly the various anatomical means by which the loss of water is prevented or controlled, have received special attention, and still form the usual subject matter of observation and discussion.

These general and easily ascertained facts are by no means unimportant, and it is a decided advantage to botanical science that they have been recorded in such numbers. A far more important fact has become increasingly evident, namely that plants living together under present day desert conditions have each a history and character of its own, expressed in peculiarities of habits and physiological activities, and evidence is not wanting that, with changing and most complicated interrelations of organism and environment, through the long period in which each species has presumably been in the making, these peculiar habits and activities have been acquired.

But apart from all theoretical considerations, it is certain that a fairly intimate knowledge of even a limited number of desert species brings the conviction that no general statement is an adequate expression of the biological relations of any one of them, that each is a law to itself, and that its actual relations to the environment must be determined for each species by critical study of its own structural and physiological characteristics, one by one. It is from this point of view that the present study has been undertaken, and for this purpose certain desert shrubs have been chosen—the creosote bush, palo verde, and mesquite—all of which possess, each in its own way,

remarkable adaptations to desert conditions, and present striking examples of survival in a region that has passed from widely different conditions at an earlier geological period to its present extreme
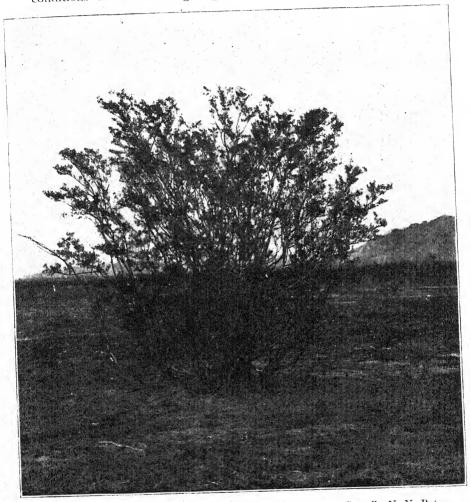


FIG. 1.—*Covillea tridentata*, near Tucson, Arizona.—From Contrib. N. Y. Bot. Gard. No. 46. Plant World 6: *pl. 35.*

aridity. Work on these several species is now under way at the Desert Laboratory of the Carnegie Institution, and as yet is incomplete. It is thought best, however, to embody in the form of a report

of progress the following notes on the creosote bush and its relations to water supply.

The creosote bush, *Covillea tridentata*, is, as is well known, one of the most characteristic species of the Lower Sonoran zone, and through its wide range, from California eastward to Colorado and Texas, and southward into Mexico, it is perhaps, of all the species of this zone, the one most constantly present and most firmly established (*fig. 1*). It occupies extended areas where its removal would leave a bare waste, but at the same time shares, on mesa and foot-hills, a great variety of soils and exposure with other species that exhibit far less capacity of accommodation than itself.

This power of accommodation is particularly noticeable as regards water supply. One has only to pass from the mesa east of Tucson, for example, to the low ground of the Rillito near Fort Lowell, observing the specimens of creosote bush as he goes along, to be convinced that the differences presented by them are due to the meager supply of water in the one case and its abundance in the other. More striking still are the changes that take place when individual plants are well watered. In contrast with the specimens around them to which no water is given, their leaves become deep green and undergo a marked increase in size, while the whole plant presents the appearance of robust health and remarkable vigor, very different from the pinched specimens with narrow, pale leaves, branches more or less defoliated, and other marks of a struggle that, however successful, is manifestly one of great severity. Plants that have been well watered for a period of years are far more fruitful than their companions standing in dry ground near by, and from their vigor, fruitfulness, and habit of retaining a greater number of healthy leaves and branches, there can be no question as to which is the normal condition; the creosote bush reaches its normal development where there is a full supply of water; arid conditions are indeed tolerated to a remarkable degree, but the plant is dwarfed and suffers in other ways while it endures them (*fig. 2*).

These facts, though matters of every day observation, are highly significant. Provisionally they may be interpreted as indicating that the creosote bush, living over much of the territory where it is now found from the period of maximum precipitation to the present time,

has acquired habits that enable it to withstand excessive drouth, but
has never lost its capacity to absorb and use large quantities of water,
and attains its best development only under such conditions.

The readiness with which this species accommodates itself to an
over-supply of water is shown by a simple experiment. Seedlings
of Covillea were grown in a flower pot, and after they had made a
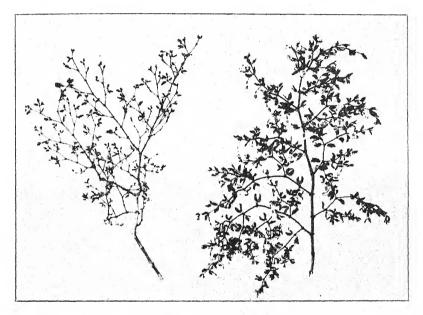


FIG. 2.—Branches of Covillea; on the right from a well watered bush near St.
Mary's Sanatorium, north of the Desert Laboratory; on the left from the exceedingly
dry soil of the mesa close by.

good start were set into a can of water, the bottom of the pot having
been broken through in several places. After three or four weeks
it was found that some of the roots had grown down into the water
and, in contrast with those growing in the soil, had taken the form of
water roots, being entirely destitute of root-hairs. The epidermal cells
exhibited plasmolysis with a 4 per cent. solution of potassic nitrate,
thus indicating their capacity for active absorption. Seedlings
grown in the Geneva tester also sent their primary roots down into
the water without apparent injury. It is plain, then, that the roots of

Covillea are capable of growing in water, at least for a time, and carry-
ing on normal absorption there.

In order to observe the effects of too great and too small a supply
of water on plants growing in soil, seeds were sown in two receptacles
measuring $23^{cm}$ in depth, and were treated as nearly alike as possible
except as to the amount of water given to them.   Both stood where
they received sunlight through a wire screen during the entire day.
One lot received a very large amount of water, manifestly much more
than they required, and the other lot was given very little, so little
that at times they seemed in danger of drying up.   At such times
they were given a little more water, after which it was withheld again.

All the plants flourished, but in the course of a few weeks there
was a marked difference between those that had received an exces-
sive supply and the ones that had received a meager supply of water.
April 12th, eight weeks after the seeds were sown, the plants were
carefully washed and examined.   The seedlings of both lots pre-
sented a fine, healthy appearance, and the roots of both had reached
the bottom of the receptacle in which they were growing and had
spread out upon it.   They differed most conspicuously in the develop-
ment of stems and leaves *(fig. 3)*.   Those that had received an
excessive amount of water measured approximately $2^{cm}$ more in
height than those to which a meager supply had been given, and the
leaves were both larger and more numerous, numbering from 6 to 10
in representative specimens of the former as against 4 to 8 in the
latter; while the largest leaflets in the two lots measured respectively
1.4 and $0.8^{cm}$ in length.   Neither lot showed as strong a development
of the root system as plants grown under the same conditions to which
an abundant, but not maximum, supply of water had been given.
Microscopic examination showed that while both lots were charac-
terized by abundance of root-hairs, these were most numerous and
better developed on the roots that had received little water.

It will be instructive to compare with this the record of two other
lots of seedlings that had been under observation for a period of seven
weeks, during which one lot had been given an oversupply of water,
while the other received very little.   On March 31st, when they were
taken up and washed free from the soil in which they had grown,
it was found that the plants to which little water had been given had

a strong and well-developed root system, but that this was very poorly developed in those that had received much water. It was noticeable, too, that while the latter were not altogether destitute of root-hairs, they had not produced them in anything like the abundance characterizing those that had been given little water, there being long stretches on which no root-hairs whatever were to be seen. Both lots of root-hairs showed plasmolysis of epidermal cells near the tip of the fresh root, and of the adjacent root-hairs, with 3 per cent. solution of potassic nitrate, but farther back in both cases plasmolysis was effected with difficulty or not at all. As for the parts above ground, both lots of seedlings had grown well, but those that had been given too much water were of a decidedly lighter green, approaching a sickly color.

From these and other observations it appears that when given an excessive quantity of water seedlings of Covillea make a remarkably rapid growth above ground, but produce a less number of root-hairs than those that have a meager supply, besides show-
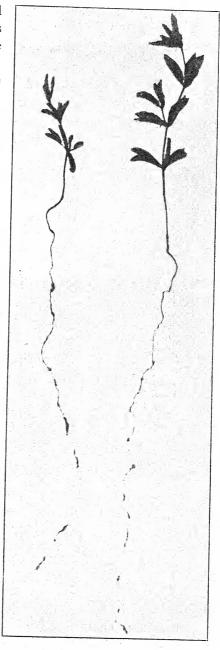


FIG. 3.—Seedlings of Covillea eight weeks old, showing effect of excessive and meager water supply.

ing other differences that may be passed over at present.   The capital fact, however, is that this species, whether as seedling or mature plant, exhibits an endurance of extremes in the matter of water supply that apparently very few species not possessing a storage system or its equivalent have attained.

This ready adjustment to differences of water supply, manifested not only in power of endurance but also in rate of growth and in other particulars, might naturally be expected to find expression in a corresponding varying rate of transpiration; it becomes, therefore, a matter of special interest to determine the habits of the creosote bush in this respect, particularly after long periods of drouth.   Accordingly a series of experiments were conducted in which the hygrometric method of determining transpiration, suggested by Dr. D. T. MacDougal was chiefly employed.[1]   By permission of the Desert Laboratory some of the results are here given in advance of publication elsewhere, in which a full account of methods employed by Dr. W. A. Cannon will be given by him.

At the time these experiments were undertaken, late in April, extremely dry conditions, both of atmosphere and soil, had long prevailed.   The rainfall since September 1903, a period of nearly seven months, had aggregated only one inch, spring flowers had failed to appear, and during nearly all of the winter and spring an intolerable dust had filled the roads and risen into the air.   Under such circumstances it might naturally be expected that transpiration on the part of every plant not artificially watered would be reduced to a minimum; the facts of the case, however, by no means warrant this conclusion.

Two specimens of Covillea were selected, one on the hill a little to the northward of the laboratory, the other at the foot of the hill in the same direction.   The former presented the fresh appearance exhibited by most of the creosote bushes near the laboratory, indicative of a water supply, however limited, in excess of that in the plain below, where the bushes looked dull and dried-up, as if subjected to most severe conditions, to which it seemed as if they must succumb.

[1]This consists essentially in direct reading of a specially constructed hygrometer placed with the plant under a bell-jar, from which escape of moisture is prevented by oiled silk or a cement base.   The correction for vapor-pressure is made once for all by weighing calcium chlorid before and after the saturated air of the bell-jar has been passed through it.

TRANSPIRATION OF THE CREOSOTE BUSH.

## No. 1.   April 22, 1904.

| Time A. M. | Percentage of saturation | Temperature | Amount in milligrams |
|---|---|---|---|
| 10:51 | 17 | 26° C. | 105 |
| 10:54 | 19.5 | 27 | 121 |
| 10:56 | 22 | 27.5 | 149 |
| 10:58 | 25.5 | 28 | 177 |
| 11:00 | 29.5 | 28 | 198 |
| 11:02 | 35.5 | 28.5 | 256 |
| 11:04 | 40.5 | 29 | 300 |
| 11:06 | 48 | 29 | 355 |
| 11:08 | 54 | 29 | 398 |
| 11:10 | 60 | 29 | 444 |
| 11:12 | 64 | 29.5 | 487 |
| 11:14 | 67.5 | 29.5 | 514 |
| 11:16 | 70 | 29.5 | 532 |
| 11:18 | 72 | 29.5 | 548 |
| 11:20 | 74 | 29.5 | 564 |
| 11:22 | 75 | 30 | 582 |

## No. 2.   April 23, 1904.

| Time A. M. | Percentage of saturation | Temperature | Amount in milligrams |
|---|---|---|---|
| 8:57 | 21 | 24.5° C. | 62 |
| 9:03 | 22.5 | 25.5 | 69 |
| 9:08 | 23.5 | 25.5 | 72 |
| 9:13 | 24.5 | 26 | 76 |
| 9:18 | 26.5 | 26 | 84 |
| 9:23 | 29 | 26 | 91 |
| 9:28 | 32 | 26.5 | 104 |
| 9:33 | 35.5 | 26.5 | 116 |
| 9:38 | 39.5 | 27 | 132 |
| 9:43 | 42.5 | 27 | 142 |
| 9:48 | 46.5 | 27.5 | 152 |
| 9:53 | 47.5 | 27.5 | 165 |
| 9:58 | 49 | 28 | 173 |
| 10:03 | 50 | 28 | 178 |
| 10:08 | 49.5 | 28.5 | 183 |

The above table gives in milligrams the aggregate amounts of watery vapor transpired during the indicated periods by each of the plants under observation, and the amounts given off are represented graphically by the accompanying curves (*fig. 4*). The

readings of the hygrometer were reduced by means of the Smith-
sonian meteorological tables and the appropriate correction then
applied for the bell-jar employed.   Later experiments indicate that
the correction applied in the present case must be considered approxi-
mately rather than quantitatively exact, but this does not affect the
value of the comparisons that follow.

From the tables here given it is seen that for the time of observa-
tion the rate of transpiration of the two plants respectively was:
no. 1, 924$^{mg}$ per hour; no. 2, 102$^{mg}$ per hour.
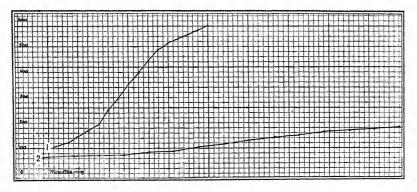


FIG. 4.—Curves showing rate of transpiration of two creosote bushes and amount
transpired by no. 1 in 31 minutes and by no. 2 in 1 hour and 11 minutes.

By counting the leaves of each plant and estimating their surface
and that of the green shoots on which they were borne, the entire
transpiring surface was estimated as: no. 1, 1533$^{sq cm}$; no. 2, 660$^{sq cm}$.

For equivalent surfaces, therefore, the rate of transpiration of no.
1, the plant on the hill, was 3.7 times that of no. 2, the plant on the
plain below.   Further experiments gave similar results.   A branch of
a creosote bush growing where the ground had been thoroughly soaked
a few weeks before by the running over of water from the tank of the
Desert Laboratory was exceptionally fresh and green, and its rate of
transpiration, for equivalent surfaces, was found to be 8.9 times as
great as that of the bush on the mesa.

From these and other detailed experiments not here reported, it
is abundantly proven that after months of excessive drouth the
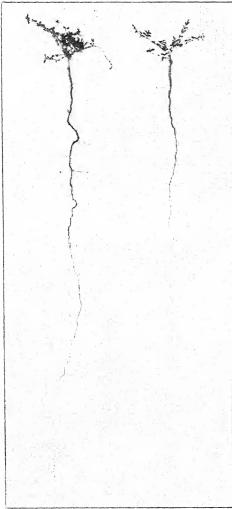
creosote bush on the mesa and foot-hills is still transpiring considerable quantities of water. The amount transpired appears to stand in direct relation to the amount of water available in the soil where the plant is growing, as is indicated by the following comparison of percentages of moisture given off by the soil when air dried.

Samples of soil were taken at depths of 20 to $30^{cm}$ below the surface from points near the plants on which the transpiration experiments were conducted. In each case the sample was weighed, then left in a shallow basin in the air, exposed to sunlight, but protected from draughts of wind, for three days, after which the weighing was repeated. It was found that the soil from the laboratory hill, taken at a depth of $30^{cm}$ below the surface, lost by air-drying during this period 8 per cent. of its weight, while that from the plain near the foot of the hill, which was much drier and in which the creosote bushes were evidently suffering from lack of water, taken from a depth of 20 to $25^{cm}$, lost at the same time 3 per cent. Another sample from the hill lost by heating over an electric stove 12 per cent. of its weight. The days when the drying was done the relative humidity of the atmosphere ranged from 20 to 27 per cent.

It is of course essential that much more extended and critical work in this direction should be carried out. Meantime the important fact is established that after months of excessive drouth the soil in which creosote bushes were living, taken only a few inches below the surface, gave up when air dried 3 to 8 per cent. of its weight of watery vapor, while a considerably higher per cent. was driven off by heat. This fact being proven, our interest chiefly centers in the capacity of the plant to utilize the available soil water after it has been so greatly reduced. This involves a study of the root system.

By way of ascertaining first general facts, the roots of creosote bushes were examined by carefully removing the earth in which they were growing, and then following their ramifications as far as possible. This is not an entirely satisfactory procedure, inasmuch as it is quite impracticable to follow the finest roots to the end without breaking them off. It is possible, however, to lay bare so large a part of the root system as to obtain a clear view of its direction of growth, mode of branching, and other characteristic features. *Fig. 5* is a photograph of two seedlings of Covillea, a few months old, that

were taken up from the mesa east of Tucson, January 13, 1904. The soil where they were dug, though rather light, is relatively deep, and it is noticeable that while the lateral roots had attained only a slight development, the tap-root had reached a depth of over $31^{cm}$ in the one case, and upwards of $53^{cm}$ in the other. A much older plant, taken up from the plain northward of the Desert Laboratory, where the soil is underlaid by rock, shows a strong development of secondary roots, and the tap-root, instead of continuing vertically downward, turns off at a small angle from the horizontal, but finally, at $80^{cm}$ distance from the main axis, turns directly downward. The lateral roots in their turn continue near the surface only a short distance, and then, in spite of the rocky nature of the substratum, turn downwards, reaching 40 to $45^{cm}$ in depth where they were broken off, though probably extending to a considerably greater depth (*fig. 6*).



FIG. 5 —Seedlings of Covillea from the mesa east of Tucson, Arizona.

The position of this particular plant with respect to those around it is instructive, and may account in part for the distribution of its

roots.   Compare the diagram, *fig. 7*, showing the position and distance of a Parkinsonia, Fouquieria, Opuntia, and another Covillea. The roots were traced more than half the distance to the Parkinsonia in one direction, and to the Fouquieria in the other.
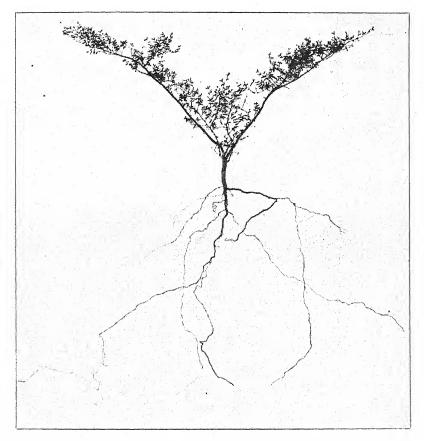


FIG. 6.—Covillea from plain to the north of the Desert Laboratory, showing character of root system.

From these and many other individual plants that have been examined, it has been found that the general plan of the root system is essentially the same in all; there is a strong tap-root which grows downwards until it meets an obstruction, or for some other reason changes its course, and slender lateral roots which run near the sur-

face for some distance.   It has not thus far been practicable to ascertain the extreme distance to which either the main or lateral roots may extend.   At the entrance of an abandoned mine the roots of a rather small plant were found exposed at a depth of $3^m$, and from their size at this point, it is probable that they extended $1.5^m$ or more
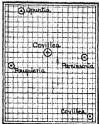


Fig. 7.—Position of Covillea with reference to plants around it, on plain north of Desert Laboratory.

farther.   Larger specimens doubtless send their roots to much greater distances.   In any case it is seen that the root system spreads widely and penetrates deeply into the earth, a disposition well adapted to secure what water is available through a comparatively wide area when there is a light rain, while the longer divisions of the root extend to the water brought by heavier rains that have reached lower levels.   Such an arrangement is all the more advantageous in view of the lack of a special storage system, the root as a whole being manifestly incapable of holding any considerable quantity of water.

The development of the root has been followed for some months by observation of seedlings grown in flower pots and larger receptacles.   Some of the results have been referred to already in the discussion of growth of seedlings as affected by water supply.   There are other facts, however, particularly the behavior of root-hairs and their relation to absorption, that require separate consideration.

Seeds germinated in a Geneva tester, so that the radicles grew in moist air, gave opportunity to observe the early formation of root-hairs under these special conditions.   As was to be expected from what has been observed in other species, they were developed in the damp air of the tester while the radicles were still very short, there being in some instances numerous root-hairs before the radicle had reached a length of $3^{mm}$.   In other cases it had grown to the length of $1^{cm}$, more or less, before any were produced.   In some cases they were close to the root tip, in others farther back, all on one side of the radicle, or projecting from all sides; in short here, where conditions were far more nearly uniform than often happens, there was such variety of habit as to render it extremely difficult to ascertain the factors actually determining the outgrowth of epidermal cells into root-hairs.

Much the same difficulty was experienced with seedlings grown in soil. In some cases the root-hairs arise thickly in complete zones, the rest of the root being free from them; in other cases, while they are abundantly produced, their distribution is extremely irregular; and in still other specimens of the same lot of seedlings the root is nearly naked, there being almost no root-hairs whatever.

In examining a large number of seedlings grown under different conditions other possibly important data in regard to this matter have been obtained, but for our present purpose it is sufficient to emphasize the well established fact that the roots of Covillea, whether growing in the lighter soil of the mesa or the heavier soil of the laboratory hill, ordinarily produce great numbers of root-hairs, and that their number becomes less if the plant is given a very large quantity of water. If grown directly in water root-hairs are altogether wanting. Whatever other conditions, then, may or may not afford the stimulus that results in the production of root-hairs in general, the quantity of water in the soil is, in the present case, a factor of prime importance. There is no doubt that the epidermal cells of the root of Covillea which would retain their original form if abundantly supplied with water do, as a matter of fact, promptly increase their surface greatly by pushing out root-hairs if the water supply is suitably diminished. Whether in this process the epidermal cell responds directly to the diminished supply of water in the soil around it, or to conditions arising from lack of water in the plant of which it is a part, is a question of theoretical interest well worthy of special investigation.

The epidermal cells near the tip of the root, whether prolonged into root-hairs or not, function as the living agents of absorption. To what extent the older root-hairs may function in the same way, or may serve rather to soak up water like a sponge, when there is an abundant supply, is a question reserved for fuller discussion than can be entered into here. We are now concerned, first of all, with the degree of force with which the undoubtedly vital agents of absorption, the living cells near the root-tip, absorb water from the relatively dry soil in which, as we have seen, the creosote bush maintains itself alive and keeps up its transpiration "stream."

In the investigation of this subject, which is still in progress, seedlings of Covillea, of different ages were carefully removed from the

soil and subjected to the action of plasmolyzing agents. A few of the experiments undertaken will be given in detail.

A young seedling, with a slender primary root $2^{cm}$ long, showed distinct plasmolysis of the epidermal cells near the root-tip within five minutes after being placed in 3 per cent. solution of potassic nitrate, and the same phenomenon was soon after obtained as far back as $1.6^{cm}$ from the end of the root. Some of the root-hairs also showed plasmolysis, but not so strongly as the epidermal cells. In the latter it was particularly distinct.

At the same time a number of good specimens growing in the Geneva tester were treated on separate slides with 2, 3, 4, and 5 per cent. solutions of $KNO_3$ at a temperature of $27°$ C. With the 2 per cent. solution plasmolysis was not observed; with 3 per cent. it was seen doubtfully or incompletely in a few of the epidermal cells; with 4 per cent. plasmolysis in many epidermal cells was strongly marked; and with 5 per cent. not only was plasmolysis promptly and strongly induced in the epidermal cells but also in some of the root-hairs. It is seen from this experiment, and from others not reported, that the root-hairs plasmolyze less readily than the neighboring epidermal cells. In the present case, while the application of 5 per cent. solution of $KNO_3$ was promptly followed by plasmolysis of some of the root-hairs, others failed altogether to exhibit the phenomenon.

Similar results were obtained from a lot of seedlings raised in soil in flower pots. They were strong and healthy, and at the end of five weeks' growth, when they were taken up for experimentation, some of them had one or two leaves well developed  Employing the secondary roots of one of the best developed individuals it was found that plasmolysis did not occur in 3 per cent. solution of potassic nitrate; that it took place promptly and distinctly in 5 per cent., both in epidermal cells and root-hairs; and that in 4 per cent. different specimens exhibited a marked difference of behavior. Of five specimens placed in 4 per cent. solution two showed plasmolysis satisfactorily, both of the epidermal cells and root-hairs, while two failed to do so, and one showed plasmolysis well in the epidermal cells but not in the root-hairs.

In these, as generally in roots subsequently examined, it was found that the older root-hairs, farther back from the tip of the root,

are very slow to become plasmolyzed, or for the most part fail alto-
gether, in solutions that readily induce plasmolysis of fresh young
cells and root-hairs near the tip. It was found, however, that some
of the older root-hairs that are not too far back from the tip exhibited
plasmolysis distinctly in a 10 per cent. solution of $KNO_3$, but the
great majority are not affected by this nor by higher percentages.

In the course of the work it was repeatedly noticed that many of
the older root-hairs presented the appearance of having undergone
regeneration, the distal end being clear or semitransparent, in con-
trast with the dark-colored basal part with its old-looking granular
contents, the clear terminal portion being irregular in outline and not
infrequently branched. In the course of experiments on an herba-
ceous plant, *Verbena ciliata*, which showed the same phenomenon
even more strikingly than did the creosote bush, it was found that
regeneration of its root-hairs could be induced readily by supplying
with water a plant from which it had been withheld for some time.
It is probable that this capacity for renewed growth on the part of
cells apparently dormant may be an important factor in the absorp-
tion of water from the soil.

To sum up briefly the observed facts regarding the absorbing
cells of the roots of Covillea: Root-hairs are, as a rule, produced
in large numbers, thus increasing many times the absorbing surface.
If the plant receives large quantities of water the number of root-
hairs falls off, and when the roots grow in water none are produced,
the creosote bush agreeing in this respect with what has been observed
in land plants generally. The undoubtedly active absorbing tissue
consists of epidermal cells and root-hairs very near the growing point
of both primary and secondary roots. These cells fail to show
plasmolysis with less than 3 per cent. solution of $KNO_3$ and are
readily plasmolyzed with higher percentages; their osmotic pressure
may accordingly be set down, with more or less variation, as equiva-
lent to ten atmospheres.

The behavior of older epidermal cells and root-hairs is such as
to throw doubt upon their functional activity as absorbing cells,
though from their observed habit of regeneration under certain cir-
cumstances, and from their action with plasmolyzing agents, there are

grounds for assuming provisionally that a considerable proportion of these are still capable of serving this purpose. If they are thus active, their osmotic force, as measured by plasmolysis, is several times that of the younger cells nearer the root-tip. It is apparent, in any case, that the osmotic force exhibited by the root-hairs and epidermal cells that are indubitably active is amply sufficient to account for the capacity of this plant to absorb water from the soils in the vicinity of the Desert Laboratory, even after such periods of drouth as those of the present year. Their absorption, however, is necessarily limited by the amount of water available. This, as we have seen, is also a determining factor of transpiration. The means by which the latter is controlled will be discussed elsewhere.

That the creosote bush is able, through its absorbing cells, to abstract continuously a certain amount of water, however small, from such dry soil as that of the desert mesa, to maintain transpiration through many months of excessive drouth, and at the same time to regulate nicely the amount of transpiration to correspond with available water supply, while all the time it is capable of living and does live as an ordinary mesophyte when given a suitable supply of water, is a remarkable fact. Its explanation involves more perfect knowledge not only of the physiological habits now under investigation, but also of the geographical history of the species, which still remains to be written. It need hardly be said that the data for both are to be sought first of all in the desert where this plant is at home.

I desire to express my sincere thanks to Dr. W. A. Cannon, the resident investigator of the Desert Laboratory, and to Messrs. Coville and MacDougal of the Advisory Board for the admirable facilities that have freely been placed at my disposal.

Desert Botanical Laboratory,
        Tucson, Arizona.

# BRIEFER ARTICLES.

## NOTES ON NORTH AMERICAN GRASSES. III.

### AGROSTIS STOLONIFERA L.

IN view of the recent tendencies to base species so far as possible upon type specimens, or in the absence of such specimens upon a definite idea to be interpreted from references to the older authors, it becomes necessary to investigate carefully the bases upon which are founded the Linnaean binomials. Two species of Agrostis are here considered.

*A. stolonifera* was described in the first edition of Linnaeus's *Species Plantarum* as follows (p. 62, under the second division, MUTICAE):

*stolonifera.* 7. Agrostis paniculae ramulis divaricatis muticis, culmo repente, calycibus aequalibus.

        Agrostis culmo repente foliis radicalibus breviore, folii suprema vagina ventricosa, flosculis muticis. Roy. ludgb. 59. Fl. suec. 62 (61).

        Agrostis culmo repente vagina supremi folii ventricosa. Roy. ludgb. 59. Dalib. paris. 23.

        Gramen caninum supinum minus. Scheuch. gram. 128. Habitat in Europa. ♃

There are three factors which enter into the determination of the type of a species: the specimen or specimens from which the description was drawn, the synonyms and citations given in the original description, and the description itself. Establishing types for Linnaean species is complicated from the fact that the descriptions may be not original with Linnaeus. His work has been that of an editor who has taken material at hand and rearranged it in accordance with his system of binomial nomenclature. Frequently he merely attached a trivial or specific name to species already well known under a polynomial designation. The older authors were not accustomed to give citations of definite specimens or definite localities. Let us examine in detail the data for determining the type of *Agrostis stolonifera*.

1. *The specimens.*—In the Linnaean herbarium (in the rooms of the Linnaean Society of London) there is only one specimen labeled with this name. This is from "Attica" and is marked in the handwriting of Linnaeus himself. This specimen is what has been going under the name of *A. ver-*

*ticillata* Vill.   The species is common in southern Europe, but is not found
in England or the Scandinavian countries.   I found no other specimen
labeled *A. stolonifera,* although Munro states that there was also one marked
thus which was a form of *A. alba* (Proc. Linn. Soc. London, Bot. **6**: 40.
"The Herbarium contains one of the forms of *A. vulgaris,* which is called
*stolonifera,* the Fiorin Grass; another, marked *stolonifera,* by Linn., is *A.
verticillata* Vill.").

   2. *Synonyms and citations.*—The first synonym is from Linnaeus's
*Flora Suecica,* p. 23, no. 61 (1745).   The citation is as quoted, but lacks
the words "flosculis muticis."   The description agrees with *A. verticillata*
Vill., especially "folii supremi vagina ventricosa."   To the description in
this work is added:

   Gramen caninum supinum minus.   Scheuch. hist. 128.
   Agrostis stolonifera vulgo.
   Suecis Kryp-hwen.
   Habitat in agris incultis ubique praefertim Upsaliae.

   The reference here to Scheuchzer is the same as given in the *Species
Plantarum.*   The description in Scheuchzer's *Agrostographia* is quite full
and agrees well with *A. verticillata* Vill.   Scheuchzer gives references to
Bauhin, but the descriptions of the latter author are less satisfactory.

   It is to be noted that the first citation given by Linnaeus (*Sp. Pl.*) is
"Roy. lugdb. 59."   This is an error, as this does not appear in Royen,
*Flora Leydensis,* the work referred to.

   The second citation (L., *Sp. Pl.*) is correctly quoted from Royen.   This
is also referred to "Dalib. paris. 23."   This is also an error, as the first
citation appears here.   It appears then that the authorities "Roy. lugdb.
59" under the first citation, and "Dalib. paris. 23" under the second cita-
tion should be interchanged.   As the description in Dalibard, *Flora
Parisiensis,* quotes Linn. *Fl. Suec.* 61, this still leaves the *Flora of Sweden*
as the basis of the first synonym.   It may be remarked that Dalibard also
quotes the description from Royen and "Gramen caninum supinum
minus."   Royen quotes a polynomial from Ray's *Synopsis* which refers
to an Irish plant, probably some form of *A. alba.*

   Going back to the *Flora of Sweden,* we find as the first synonym the
citation from "Scheuch. hist. 128," which is *A. verticillata* Vill.

   All the evidence under the head of synonymy, then, is in favor of *A. verti-
cillata* Vill. as being the basis of Linnaeus's *A. stolonifera,* except that the
description appears in a *Flora of Sweden,* where *A. verticillata* does not occur,
or at least not commonly, and yet is said to be common there in unculti-
vated fields.   Linnaeus evidently had confused two species—what we have

been calling *A. alba* and *A. verticillata*. It would seem best to dispose of this conflict by admitting that Linnaeus committed an error of determination in identifying the Swedish plant with the form common in southern Europe.

In this connection it is interesting to note that Linnaeus has little to say about *A. alba* in the *Species Plantarum*. The description is:

9. Agrostis panicula laxa, calycibus muticis aequalibus. Roy. lugdb. 59. Habitat in Europae nemoribus.

Royen adds as a synonym "Gramen nemorosum, paniculis albis. Vaill. par. Tab. 17. f. 5. opt."

The figure in Vaillant, however, is not an Agrostis, but apparently a species of Poa.

There are several sheets of *A. alba* in the Linnaean herbarium, one of which is marked in his own handwriting and is the common form of what has been so called.

3. *Description.*—The part relating to the divaricate panicle refers better to *A. alba*, especially the variety *vulgaris*, but the part relating to the creeping culm and the equal calyx refers better to A. *verticillata*.

Taking everything into consideration, it appears that Linnaeus confused two species, but we are justified in taking the specimen in the Linnaean herbarium as the type of *Agrostis stolonifera* L.=*A. verticillata* Vill.

The identity of the Linnaean specimen has been pointed out by earlier authors, *e. g.*, Parlatore *Fl. Ital.* 1: 180.

<center>AGROSTIS RUBRA L.</center>

The description given in the *Species Plantarum* (p. 62) is:

*rubra.* 4. Agrostis paniculae parte florente patentissima, petalo exteriore glabro terminato arista tortili recurva. Fl. suec. 60. Dalib. paris. 24.

Agrostis panicula inferiore verticillatim laxa; superiore contracta. Fl. lapp. 46.

Gramen serotinum arvense, panicula contracta pyramidali. Scheuch. gram. 148.

Habitat in Europae arenosis subhumidis.

1. *Specimens.*—In the Linnaean herbarium there is one sheet marked by Linnaeus, but the plant is a panicle of what appears to be *Sporobolus junceus* of our southern states. As this does not accord with the description or citations, it may be withdrawn from consideration, as there is evidently an error somewhere.

2. *Synonymy.*—In the *Flora Suecica* the three citations appear as given in the *Species Plantarum*, and in the same order, but "Dalib. paris. 24" is omitted, as this is a subsequent work (1747). There is added, however:

Gramen serotinum arvense, spica laxa pyramidali.  Raj. hist. 1288.  Vaill.
paris. 88.

Suecis Röd-hwen.

Habitat ad ripas lacuum & in partis depressis ubique.

In the *Flora Lapponica*. p. 27, no. 46 (1737) we find in addition to the
quotation given above (in which *injerne* replaces *injeriore*):

Gramen segetum arvense, panicula contracta pyramidali.  Raj. hist. 1288.
Scheuch. hist. 148.

α Ad ripas lacuum, tempore autumnali; rufescens occurrit.

β Panicula, dum floret, secundum verticillos explicatur horizontaliter patens;
   contracta superius in eadem nondum florente.

The references to Ray and Scheuchzer are based on *Milium lendigerum*,
as are also those of Vaillant and two additional references which he gives.
"Plukenet Phytographia Tab. 33, fig. 6," and "Tournefort Institutiones
Rei Herbariae 515."

3. *Description.*—There is no description in the *Species Plantarum*
aside from the synonyms given, but the habitat "in arenosis subhumidis"
would not seem to apply to the plant going under the name of *A. rubra* L. =
*A. borealis* Hartm., which is an alpine grass.

The description given in the first citation, "Fl. Suec.," does not apply
to *A. borealis* Hartm., as the flowering glume ("petalo exteriore") is said
to terminate in a recurved twisted awn.  The awn in *A. borealis* arises from
the back of the glume.  It is to be noted that Linnaeus described the next
species, *A. canina*, as having the awn dorsal (Sp. Pl. 62; Fl. Suec. 392, no.
1138).  As the awn is terminal in *Milium lendigerum*, it is probable that
this part of the description was based upon that species, which he has in
some way confused with the Swedish plant.  It is also to be noted that he
describes in his *Flora of Lapland* only two species of Agrostis, *A. capillaris*
and the species under consideration.  It has been pointed out by several
European authors that Linnaeus evidently confused two or more species
under *A. rubra*, one of which was *A. vulgaris*.  This, added to his error
of determination in identifying the Scandinavian plant with *Milium lendi-
gerum* of southern Europe and the consequent mixing of synonyms, has made
it impossible to determine with any definiteness the type of *A. rubra*.  For
this reason it is best to take up the next available name, *A. borealis* Hartm.
Skand. Fl. Ed. 4. 23. 1843.

Linnaeus evidently discovered his error in regard to *Milium lendi-
gerum*, for in the second edition of the *Species Plantarum* he described this
and based the name on "Raj. Hist. 1288, Scheuch. Gram. 148."  He also

cites "Pluk. Tab. 33 fig. 6," but forgets to withdraw this citation from his synonymy under *A. rubra*.—A. S. HITCHCOCK, *U. S. Department of Agriculture.*

## CARL SCHUMANN.

### A BIOGRAPHICAL SKETCH [1] (WITH PORTRAIT).

KARL MORITZ SCHUMANN was born June 17, 1851, in Görlitz (Silesia). After attending the Real-Gymnasium of his native town until 1869, he studied at the universities of Berlin, Munich, and Breslau, devoting himself at first to chemistry, later principally to botany and related sciences.

The doctor's degree was conferred upon him by the University of Breslau, July 19, 1873, the title of his dissertation being *Dickenwachsthum und Cambium.*

A year previously he had accepted a position as assistant to Professor Dr. GOEPPERT, the famous authority on fossil plants, which he held until the spring of 1876. In November 1875 he passed with honor the Prussian state examination, and shortly afterwards took up the profession of teaching. For eight years, beginning with 1876, he taught in the Real-Gymnasium "Zum heiligen Geist" in Breslau. A work entitled *Kritische Untersuchung über die Zimmtländer*, which he wrote during this time, showed as much historical and geographical as scientific knowledge. On account of this book he was called in the summer of 1884 to Berlin, where he was appointed curator of the Berlin Botanical Museum recently established by A. W. EICHLER. In June 1892 he was appointed professor, and in the spring of 1893 he obtained the right to deliver academic lectures on botany in the University of Berlin. On March 22, 1904, death closed his full and fertile life.

The contributions by which SCHUMANN advanced scientific botany are extraordinarily numerous, and as the work of a single man most astonishing. We may divide them into purely systematic, phytogeographic, morphological, biological, pharmaceutical, didactical, biographical, and the work of reviewing.

[1] Excerpt from a manuscript of Professor Volkens.

In MARTIUS's *Flora Brasiliensis* he worked up Triuridaceae, Cactaceae, Sterculiaceae, Tiliaceae, Malvaceae, Bombacaceae, Bignoniaceae, and Rubiaceae; and for ENGLER and PRANTL'S *Die natürlichen Pflanzen-jamilien*, in addition to the above mentioned families, he treated Chlaena-ceae, Elaeocarpaceae, Asclepiadaceae, and Apocynaceae. Of mono-graphs there exist from his pen Marantaceae, Musaceae, and Zingiberaceae in ENGLER's *Pflanzenreich;* and Sterculiaceae in ENGLER's *Monographien ausgewählter afrikanischer Pflanzenfamilien.* As an independent work he published the *Gesamtbeschreibung des Cacteen* and *Iconographia Cacta-cearum.* The new species he described may be numbered by hundreds, probably by thousands, especially notable among them being those of tropical Africa. For the most part they were published in ENGLER's *Botanische Jahrbücher.*

Among the phytogeographic works of SCHUMANN are *Flora von Kaiser-Wilhelmsland*, in which he was assisted by LAUTERBACH; *Flora von Neu-Pommern;* and *Flora der deutschen Schutzgebiete.* Of his biological and didactical treatises the most important are his investigations on myrmeco-philous plants, and two text-books on systematic botany, *Lehrbuch der systematischen Botanik* and *Prakticum für morphologische und systemat-ische Botanik*, the latter appearing after his death. Among his pharma-ceutical contributions are the new edition of BERG and SCHMIDT's *Atlas der officinellen Pflanzen*, observations on Hydrastis and Podophyllum, and several articles on plants yielding caoutchouc and kola. Among his biographical works are numerous necrologies of well-known botanists; and his editorship of JUST's *Jahrbuch* must not be forgotten.

The starting-point of SCHUMANN's morphological investigations was his studies on the development of the organs of flowers. These interested him most deeply and allowed him to show in a striking manner his masterly descriptive powers. On observations of this kind were based his papers on the borragoid, on the monochasia, on the ramification of Pandanus; as well as his studies in regard to the morphology of flowers, the results of which he published in his voluminous work *Ueber den Blütenanschluss.* SCHUMANN was the first to point out the untenableness of the prevailing theory of the purely formal morphology of flowers. He showed that mere comparison and the consideration of teratological facts lead to the most erroneous ideas, if it is desired to account for the position of the organs in their causal connection. The only way to advance the science of the morphology of flowers, he claimed, is to apply the principles which SCHWEN-DENER had employed in his mechanical theory of the position of the leaves in relation to the vegetative organs. It must not be concealed that SCHU-

MANN later, in his *Morphological Studies*, I and II, did not strictly adhere to this view, and that he even began to doubt the basis of the mechanical theory of leaf position. To him, however, belongs the honor of having immensely advanced botanical morphology by means of a wealth of single observations, at a period when this branch of science elicited nowhere else the interest necessary to produce results.

When we review the life-work of SCHUMANN we find ourselves confronted by a problem. How did a man to whom every day brought new professional duties still find time to occupy himself so fully with scientific work? The solution is to be found in his creative impulse, in his gift of easy comprehension, in his powers of clear expression, and in his conscientious desire to crowd into his daily task the full force of all his intellectual activities.

The honors conferred upon SCHUMANN were not in proportion to his scientific importance or his distinguished gifts as a teacher. He was not made unhappy by this, but contented himself with the recognition of his colleagues, and found abundant compensation in the love and veneration everywhere paid him for his human qualities, his bright and cheerful nature, his courtesy, and his never-failing willingness to help.—*Translated by* J. PERKINS.

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## A CORRECTION.

IN THE June issue of the BOTANICAL GAZETTE, Mr. PLOWMAN publishes an article on "The celloidin method with hard tissues," stating that it has been "developed and perfected by Dr. E. C. JEFFREY," and that it "has been incompletely described at second and third hand elsewhere," in this connection calling attention to my book on *Methods in plant histology*. The collodion method was published in 1879, the celloidin method in 1882, and for nearly two decades both methods have been matters of text-book knowledge. Since I have used celloidin very little, except for woody tissues, I have made no effort to improve the method, but have simply followed more or less exactly and have described with slight variations the procedure in vogue in Professor EYCLESHYMER'S classes at the University of Chicago since 1893. Consequently, Mr. PLOWMAN is mistaken in assigning my account so high a rank as second hand, when in reality it is an accumulation so old that it cannot claim to be anything more than an ordinary text-book account, culled from older text-book accounts. Indeed, the use of hydrofluoric acid is the only essential addition by Mr. PLOWMAN to the long used celloidin methods.—CHARLES J. CHAMBERLAIN.

# CURRENT LITERATURE.

## BOOK REVIEWS.

### Physiological plant anatomy.

THAT physiological anatomy is not one of those subjects that may be regarded as completed, so far as important new researches are concerned, is illustrated when one makes a comparison of the second and third editions of HABERLANDT's well-known work.[1] The first edition of this important work appeared in 1884, and since then there has been no excuse for the presentation of anatomy in a dead and formal manner. A second edition was issued in 1896,[2] and now in a still shorter time we are favored with a third edition. In this the pages have been increased from 550 to 616, and the figures from 235 to 264. While the general plan of the work resembles that of the second edition, there are many noteworthy additions in most of the chapters, and the latter part of the book has been rewritten, because the knowledge of these topics has been almost revolutionized, and in large part through the discoveries of the author himself.

The introductory chapters on plant cells and tissues, and embryonic tissues have suffered little change; a new section is added, dealing with the size of cells. In the chapter entitled "Das Hautsystem," there is a new subsection on secondary epidermal functions. Anthocyan receives a fuller treatment, while the recent studies of DAMM on perennial epidermis, and TITTMANN on the regeneration of wax rods are summarized. Little change in the treatment of the mechanical tissues is to be seen, except for the introduction of the experimental work of VÖCHTING, BALL, and WIEDERSHEIM. More is added regarding the absorption tissues. There is a new paragraph dealing with absorption in insectivorous plants, and SCHAAR's discovery of a cambium layer in the thallus of Rafflesia is fully described. The author clings to his former views regarding the functions of rhizoids and aerial roots, and fails to accept as conclusive the work of KAMERLING, PAUL, and NABOKICH. It is disappointing to see no essential change in the treatment of mycorhiza, a topic concerning which vastly more is known than in 1896. In the chapter entitled "Das Assimilationssystem," NORDHAUSEN's work on palisade cells is considered, but the excellent work of GRIFFON and others receives little or no mention. Latex tubes are still regarded as conductive vessels; ROTHERT's studies on the structure of the fibrous thickenings of conductive vessels give material for an interesting additional statement. The most notable

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[1] HABERLANDT, G., Physiologische Pflanzenanatomie. Dritte, neubearbeitete und vermehrte Auflage. Imp. 8vo. pp. xvi+616. *fig. 264.* Leipzig: Wilhelm Engelmann. 1904.

[2] See review in BOT. GAZ. **23**:472. 1897.

additions to the chapter on storage tissues are a description of JÖNSSON's peculiar "mucilage cork," water storage cells derived from phellogen; and a note regarding FISCHER's work on inulin.  Much new material is found in the chapter on aeration tissues: RACIBORSKI's breathing organs in early leaf stages; WESTERMAIER's remarkable but questionable lung-like organ on Sonneratia roots; BROWN and ESCOMBE's brilliant work on gas diffusion; KAMERLING on liverwort pores; PORSCH on adaptations for securing permanent closure in the stomata of submerged hydrophytes; and DEVAUX on lenticels.  HABERLANDT disagrees in part with DEVAUX's results, and does not consider the paper as very important; he also rejects WIELER's results concerning aerenchyma.  There is an excellent new figure of a lenticel, and another interesting new figure is that of the stoma of Nipa.  Another chapter that is rich in new matter is that on "Die Sekretionsorgane und Exkretbehälter."  The hydathode figure is much improved, and the rich recent literature on hydathodes is well summarized; little or no credit is given to the views of SPANJER and LEPESCHKIN, insofar as they are contrary to the views formerly expressed by the author.  One of the notable additions here is the discovery of glands in Ruta which discharge to the exterior by means of slits that arise between external cells.

Far the most notable change of the new edition is to be found in the expansion of the old eleventh chapter, entitled "Apparate und Gewebe für besondere Leistungen."  The material there presented is now considered in three chapters, entitled respectively "Das Bewegungssystem," "Die Sinnesorgane," "Einrichtungen für die Reizleitung."  In the chapter on motor tissues there is a fuller discussion of the hygroscopic tissues.  There is an entirely new section on cohesion mechanisms, embracing the contributions of KAMERLING, STEINBRINCK, and SCHRODT, regarding the movements that are due to the cohesive force of water in the cell lumina of fern sporangia and liverwort elaters.  Much is also added in the section dealing with living motor tissues, embracing in particular the contributions of FITTING, SCHWENDENER, MÖBIUS, PANTANELLI, and HABERLANDT.  The topic which has been most completely recast is that of the sense organs, and in this field HABERLANDT himself has been a pioneer and major contributor.  This chapter for the most part may be regarded as a summary of the volume on this subject which has but recently come from the author's hand.  After an introduction treating the general characteristics of sense organs in plants, there is a specific description of the tactile pits of Cucurbita and Drosera, the tactile papillae of various stamen filaments, and the tactile hairs of Centaurea, Biophytum, Mimosa, Aldrovandia, and Dionaea.  Then follows an account of the sense organs for the perception of gravity and light stimuli; here there is a description of the statolith organs of plants, in which there is incorporated the chief results of NĚMEC, NOLL, JOST, DARWIN, and particularly those of the author.  In the chapter on motor mechanisms, there is an entirely new section dealing with the intercellular and intracellular fibrillar structures, to which NĚMEC in particular has devoted so much attention.  HABERLANDT

still holds to his former view concerning the motor mechanisms of Mimosa, in spite of the doubt cast upon his theory by the work of MacDougal and Fitting.

The noteworthy changes that are to be found in this third edition make it necessary for all libraries. Many among us may not accept the teleological views that are to be found throughout the work, and it may occasion disappointment to find at several points, as stated above, that the author maintains his own unstable theories in the face of what will appeal to most botanists as conclusive proof against them. In particular, it is highly doubtful if we may longer believe in the condensing power of the aerial roots of orchids, conduction by the shortest route as explaining the elongation of palisade cells, the conductive function of latex tubes, the secretive rather than storage function of aleurone, or the hydrostatic propagation of stimuli in Mimosa.

The teleological views of the author are apparently not merely conveniences of expression, but purpose in plant structures appears to be regarded as an objective reality, which operates as a cause in the development of plant organs and tissues. As a consequence, it may not be surprising that the author is almost violent in his opposition to the contributions of such men as Devaux, Spanjer, and Wieler, and gives no place at all or at most inadequate consideration to the work of such men as Griffon, Bernard, and Friedel. The trend of modern investigation is certainly away from the idea that purpose is the directive factor in the evolution of structures, as well as from the idea that all structures must have a definite and advantageous function. However, the vast majority of structures are certainly useful, and the study of function in relation to structure gives life and vitality to what is otherwise a dead and profitless study to most students. And for this reason Haberlandt's work fills a place that is taken by no other work. For this reason, too, it is much to be hoped that there will soon be available a translation of this third edition.—H. C. Cowles.

### Smoke and vegetation.

There have been a number of treatises dealing with the injurious effects of smoke on vegetation, but we are now favored with a monographic treatment of the subject by Haselhoff and Lindau.[3] There are first some general considerations on the origin of smoke, the characteristics and extent of its injuries to plants, the various causes of the formation of leaf spot, and the comparison of normal plant characteristics with injuries due to smoke. The body of the work deals with the injurious smokes and vapors in detail. Particular attention is paid to the effect of sulfurous and sulfuric acid vapors. Injurious effects are found to be associated chiefly with the foliage organs; little or no harm comes to the plant through vapors which may have been absorbed by the soil. Harmful effects are made evident through the formation of leaf spots, the death of leaves and young branches, the disorganization of chloroplasts, plasmolysis,

[3] Haselhoff, E., and Lindau, G., Die Beschädigung der Vegetation durch Rauch: Handbuch zur Erkennung und Beurteilung von Rauchschäden. Imp. 8vo. pp. viii+412. *figs. 27.* Berlin: Gebrüder Borntraeger. 1903. *M* 10.

an increase of tannin deposits, and a reduction in the annual ring. An important point is that the stomata play no particular part in the absorption of the injurious vapors; the whole leaf appears to be involved in the process.

Plants vary widely in their power of resistance to noxious vapors; this might be anticipated in the case of different plant species, but it is strongly true as well among different individuals of the same species. Harmful effects are accelerated when there is an increase of light, heat or drouth, and as might be supposed therefrom, one of the first signs of injury is a drying out of the leaf, due to an impeded circulation of water. In a similar manner, though much less fully, the injurious influences of other smokes and vapors are discussed, *e. g.*, chlorin, hydrochloric acid, hydrofluoric acid, nitric acid, acetic acid, ammonia, hydrogen sulfid, bromin, tar, pyridin, phenol, fog, asphalt, illuminating gas, and dust. It will be seen from the list of subjects treated that the monograph considers all atmospheric elements apart from those which are commonly regarded as normal, whether or not they may be classed under the head of smokes or vapors. The book abounds in examples that have been taken from a wide field experience. For this and other reasons, the work will prove of great value to foresters, and to all who cultivate plants in the vicinity of cities or factories. And the botanist also will find here for the first time, perhaps, the injurious effects of smokes and vapors presented in such a way as to permit of ready reference.—H. C. Cowles.

### Classification of flowering plants.[4]

Mr. A. B. Rendle has undertaken to present to the somewhat advanced student "a systematic account of the flowering plants," and the first volume, now before us, comprises the gymnosperms and monocotyledons. It may be said that the emphasis is laid upon classification, as the title would imply, rather than upon morphology. The essential morphology of the great groups is outlined briefly, but systematically and clearly, the modern point of view and terminology largely dominating, although it did not seem possible for the author to eliminate sexual terms entirely from the terminology of sporophytic structures.

The author regrets that "the means available did not allow of the preparation of large figures," for this feature of the book is out of all proportion to the value of the text. However, he has done remarkably well with the limitations that were set for him.

One of the most interesting chapters in the book is the first one, dealing with the evolution of plant classification. The subject is one which the author's experience has peculiarly fitted him to treat, and this chapter is one of the best compact presentations of it for the general student that we have seen.

Naturally the large usefulness of the book is in its full account of the plant groups, in which there is brought together a mass of information that will be of

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[4] Rendle, Alfred Barton, The classification of flowering plants. Vol. I. Gymnosperms and Monocotyledons. 8vo. pp. xiv + 403. Cambridge Biological Series. Cambridge: The University Press. 1904. $3.50.

great service to those who are not extreme specialists in the classification of seed-plants. The collated literature is supplemented by the large experience of the author, so that in a sense the presentation is distinctly a fresh one.

This book and others like it serve to emphasize the increasing differentiation between the specialists in morphology and those in classification. It is no longer possible for one man to do justice to both subjects in a single book. One or the other dominates in accordance with the larger interest of the author, and the other phase receives comparatively scant attention. In the book before us taxonomy is dominant, and only that amount of morphology is presented which is supposed to be of importance to a specialist in taxonomy. In other books morphology is dominant and taxonomy reduced to a bare outline. There is an additional complication in the case of seed-plants because of an old morphology that belongs to them. The old morphology has more dealings with taxonomy than it does with the new morphology, and will doubtless continue to be exploited chiefly by taxonomists. Anatomy has already become distinctly differentiated as a subject, and the morphologist of either kind has learned to touch it very lightly.—J. M. C.

## MINOR NOTICES.

THE ISSUE of the twelfth edition of PRANTL'S *Lehrbuch der Botanik*, under the editorship of DR. PAX,[5] indicates that this book holds an assured place among German text-books. The present edition has been very slightly enlarged, though brought into line with modern work in many places. Improvements are also noticeable in many figures and some new ones are introduced.

Of its kind the book is excellent, but the kind no longer appeals to American botanists as a model. For it gives 122 pages to anatomy, 53 pages to physiology, and 279 to the dreary synopsis of plant families, which we suppose medical students and other victims of the required "allgemeine Botanik" are still forced to study—else it would hardly form so dominant a part of all German text-books. It might be well for our German friends to undertake a reform movement in botanical instruction.—C. R. B.

THE NINETEENTH PART of ENGLER'S *Das Pflanzenreich* consists of a presentation of Betulaceae by WINKLER.[6] The usual critical discussion of structure, geographic distribution, and systems of classification is followed by descriptions of 83 species recognized as representing 6 genera, all but 11 of the species belonging to Betula (37), Carpinus (18), and Alnus (17). In Carpinus 7 new species are described, and in Betula 3, but none of them belong to the American flora. Dr. BRITTON'S 4 new species of Betula recently described[7] are referred to in the *Addendum* as not examined. The conservative tendency of the work is indicated

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[5] PAX, F., PRANTL'S Lehrbuch der Botanik. 12th ed. Imp. 8vo. pp. viii+478. *figs. 439.* Leipzig: Wilhelm Engelmann. 1904.

[6] ENGLER, A., Das Pflanzenreich. Heft 19. Betulaceae von HUBERT WINKLER. pp. 149. Leipzig: Wilhelm Engelmann. 1904. *M* 7.60.

[7] Bull. Torr. Bot. Club **31**: 165. 1904.

not only by the few new species, but chiefly by the numerous varieties, especially in Alnus.—J. M. C.

To ACCOMPANY his secondary school text-books, which imply a considerable amount of laboratory work in botany. Mr. J. Y. BERGEN has prepared a *Note-book*,[8] in which he has arranged directions for experiments, chiefly physiological, with various useful suggestions to the student, intending thereby to promote neat and thorough reports of the work. Most teachers will prefer the loose-leaf notebook, which permits criticism and correction without permanently marring the record. The laboratory directions of course minimize dictation and copying, but the forms also curtail freedom and initiative which it is equally important to cultivate.—C. R. B.

MISS PERKINS[9] has published the second fascicle of her contributions to the flora of the Philippine Islands. Numerous families are represented more or less extensively, the more important contributions dealing with Marantaceae, Legum-inosae (9 n. spp.), the genus Canarium (Burseraceae) with 14 new species, Tilia-ceae (9 n. spp.), Sterculiaceae (5 n. spp.), Asclepiadaceae (by R. SCHLECHTER and O. WARBURG) with 24 new species and a new genus (*Dorystephania*), and Gramineae (by C. MEZ and R. PILGER) with 4 new species.—J. M. C.

THE SIXTH FASCICLE of Roth's *Europäischen Laubmoose*[10] begins the Bryaceae, describing, with the help of ten plates, 21 species of Webera, 108 of Bryum, and 13 of other genera. The seventh fascicle completes the Bryaceae, Mniaceae, Meeseaceae, Aulacomniaceae, Bartramiaceae, Timmiaceae, and begins the Polytrichaceae. The ten plates, however, are almost wholly devoted to Brya-ceae.—C. R. B.

MAIDEN,[11] in the fourth part of his revision of Eucalyptus, presents *E. incras-sata* Labillardière and *E. joecunda* Schauer, the description in each case being followed by discussion of synonymy, range, and affinities.—J. M. C.

## NOTES FOR STUDENTS.

PORODKO, as a result of his researches on the oxidases,[12] concludes that they probably do not take part in the process of respiration. He also contributes some facts to the technique of the guaiac reaction.—C. R. B.

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[8] BERGEN, J. Y., Notebook to accompany Bergen's text-books of botany or for general use in botanical laboratories of secondary schools. 4to. pp. 144. Boston: Ginn & Co. 1904. 75 cents.

[9] PERKINS, J., Fragmenta florae Philippinae. Fasciculus II. pp. 67–152. *pls. 1–3.* Leipzig: Gebrüder Borntraeger. 1904. *M5.*

[10] ROTH, GEORG, Die europäischen Laubmoose. 2 Band. 6 Lieferung. Imp. 8vo. pp. 1–128. *pls. 1–10.* 7 Lieferung. pp. 129–256. *pls. 11–20.* Leipzig: Wilhelm Engelman. 1904. Each *M* 4. (Parts not sold singly.)

[11] MAIDEN, J. H., A critical revision of the genus Eucalyptus. Part IV. pp. 93–124. *pls. 13–24.* Government of New South Wales: 1904.

[12] PORODKO, T., Zur Kenntniss der pflanzlichen Oxidases. Beihefte Bot. Cent. **16**:1–10. 1904.

BERNARD adds his name[13] to the increasing list of those who are unable to obtain evidence of photosynthesis outside the organism. Using various methods he "obtained no positive appreciable results."—C. R. B.

LOCK[14] has made some interesting observations upon a variety of *Turnera ulmifolia* that has become naturalized in Ceylon. The flowers are distinctly heterostylic and apparently absolutely self-sterile, and the pollinating insects are bees, notably *Apis indica*. The seeds are most commonly dispersed by the aid of harvesting ants.—J. M. C.

A NOTE in the July number regarding the experiments of KOERNICKE on radium emanations should have included reference to the experiments of DIXON, who found seedlings retarded in growth without serious injury. Experiments on cultures of 48 species of bacteria by DIXON and WIGHAM[15] showed inhibition of development, confirming the results of other observers.—C. R. B.

FRIES[16] has published an interesting article on ornithophily in the South American flora, arriving at the conclusion that there is no distinct difference between ornithophilous and entomophilous flowers, and that the same species may be pollinated as well by insects as by humming birds in one place, while in another locality either of these agents may be acting.—P. OLSSON-SEFFER.

INTERCELLULAR protoplasm in the cotyledon of *Lupinus albus* is reported by KNY[17]. This protoplasm does not seem to differ from that contained within the cells, except that it contains no nuclei, starch grains, or plastids. Ripe seeds were used in the investigations. The behavior of the intercellular protoplasm during the germination of the seed will be described in a future paper. —CHARLES J. CHAMBERLAIN.

IN A PAPER on the flora of the mountains of northern Finland, BORG[18] gives the results of his studies of the plant distribution within two of the zones occurring in these mountains, none of them higher than 1200m. The paper discusses in detail the composition of the mountian flora and the origin of its components.

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[13] BERNARD, CH., Sur l'assimilation chlorophyllienne. Beihefte Bot. Cent. **16**: 36-52. 1904.

[14] LOCK, R. H., Ecological notes on *Turnera ulmifolia* L., var. *elegans* Urban. Annals Roy. Bot. Gard. Peradeniya **2**:107-119. 1904.

[15] DIXON, H. H., and WIGHAM, J. T., Preliminary note on the action of the radiations from radium bromide on some organisms. Sci. Proc. Roy. Dublin Soc. N. S. **10**²:178-192. *pls. 16-18.* 1904.

[16] FRIES, R. E., Beiträge zur Kenntniss der Ornithophilie in der südamerikan ischen Flora Arkiv for Botanik **1**:389-440. 1904.

[17] KNY, L., Studien über intercellulares Protaplasma. I. Ber. Deutsch. Bot. Gesells. **22**:29-35. 1904.

[18] BORG, VÄINÖ, Beiträge zur Kenntniss der Flora und Vegetation der finnischen Fjelde (alpinen und subalpinen Gebirge). I. Acta Soc. pro Fauna et Flora Fennica **25**: no. 7. pp. 170.

The promised second part dealing with the vegetation will probably be of greater interest.—P. OLSSON-SEFFER.

WIESNER describes[19] casting of leaves in summer due to deficient light and to consequent interference with photosynthesis, which is distinct from a similar effect of drouth and heat and not continuous with the autumn defoliation. The loss amounts to 8–30 per cent. of the foliage in sensitive trees. It begins, in those trees which complete their leaf formation in spring, when the midday sun has reached the same elevation at which foliation was completed, whereas it is almost imperceptible in trees whose foliation extends into the summer.—C. R. B.

BEARD[20] has discussed "the track of heredity" in plants and animals, chiefly the latter. A luminous statement in reference to plants is as follows: "In the embryo-sac of Pinus, which is the gametophyte, there are only four germ-cells. In the corresponding structure in flowering plants there are perhaps three, or at most six; while, as is well known, the male gametophyte of a flowering plant is represented by one or two vegetative cells and one or two germ-cells." This may be clear to a zoologist, but its interpretation is beyond the powers of the plant morphologist.—J. M. C.

BLAKESLEE[21] has made preliminary announcement of his results in a study of the methods of reproduction in Mucorineae. It seems that zygospore production in this group "is conditioned by the inherent nature of the individual species and only secondarily or not at all by external factors." Two methods of zygospore formation are recognized, and upon this basis Mucorineae may be divided into two groups designated as "homothallic" and "heterothallic," the terms corresponding to "monoecious" and "dioecious" among higher forms. The general conclusions are that the formation of zygospores is a sexual process, that the mycelium of a homothallic species is bisexual, that the mycelium of a heterothallic species is unisexual, and that among the heterothallic species certain ones have a distinct differentiation of sex. It is interesting to note that in conjugation the swollen portions ("progametes") from which the gametes are cut off do not "grow toward each other," as commonly stated, but arise as a result of the stimulus of contact between hyphae, and are from the outset adherent.—J. M. C.

MASTERS[22] has published a synopsis of the genus Pinus, the purpose of which he states is "to add to our knowledge of the species and to facilitate their deter-

[19] WIESNER, J., Über Laubfall infolge Sinkens des absoluten Lichtgenusses (Sommerlaubfall). Ber. Deutsch. Bot. Gesells. **22**:64–72. 1904.

[20] BEARD, J., The track of heredity in plants and animals. Trans. and Proc. Bot. Soc. Edinburg **22**:126–155. *figs. 3.* 1902.

[21] BLAKESLEE, ALBERT FRANCIS, Zygospore formation a sexual process. Science N. S. **19**:864–866. 1904.

[22] MASTERS, MAXWELL T., A general view of the genus Pinus. Jour. Linn. Soc. Bot. **35**:560–659. *pls. 20–23.* 1904.

mination." The genus is limited, as is usual now, to those abietinous forms in which both shoots and leaves are dimorphic. A somewhat full discussion of the value of the histological characters often used in classification reaches the conclusion that they have no greater intrinsic value than any other characters, being useful but not infallible guides, likely to vary more than some other characters. The two great divisions proposed are TENUISQUAMAE (with relatively thin cone-scales) and CRASSISQUAMAE (with cone-scales notably thickened toward the apex). Under the former are the sections *Strobus* (10 spp.) and *Cembra* (3 spp.); under the latter the sections *Integrifoliae* (8 spp.), *Serratifoliae* (4 spp.), *Indicae* (3 spp.), *Ponderosae* (12 spp.), *Filifoliae* (7 spp.), *Cubenses* (5 spp.), *Sylvestres* (10 spp.), and *Pinaster* (11 spp.). A useful feature of the contribution is a chronological list of specific names, extending from 1753 to 1903. The author's long study of the genus makes this contribution unusually rich in facts and suggestions.—J. M. C.

TRANSEAU[23] has made a preliminary announcement of certain results in connection with the investigation of the causes of xerophily in bog plants. Using *Rumex Acetosella*, great modification in the appearance and structure of the leaves was produced by varying the conditions; for example, growing in moist conditions and in dry sand. Also, the marked xerophilous characters induced by growth in the latter substratum were also obtained by growth in an undrained wet sphagnum substratum of low temperature. Further, under these conditions the drops of oil or resin, characteristic of bog xerophytes, were formed in the epidermis and in the cells adjacent to the bundles. He concludes that these modifications in the case of the bog habitat are a response to the unfavorable conditions for absorption by the roots, due to low temperature and lack of aeration. It is also suggested that the development of palisade tissue in response to strong light is correlated with drouth rather than with light, resulting from increased transpiration. "The elongated palisade cells, therefore, are an adaptation for the ready transfer of food materials in the leaf tissues, under the stress of a reduced water supply."—J. M. C.

HABERLANDT in reexamining the perceptive mechanism of heliotropic leaves finds three types:[24] (1) those in which the lamina alone is sensitive; *e. g., Begonia discolor* and probably shade plants in general; (2) those whose lamina and petiole are perceptive; *e. g., Tropaeolum* spp., *Malva verticillata* (*fide* VÖCHTING), and probably climbing and twining plants; (3) those whose petioles or motor organs are sensitive; *e. g.*, Phaseolus. He suggests that in euphotometric foliage leaves the cells of the upper epidermis constitute a sensory epithelium for the perception of light. Sometimes all cells share alike in this function, but in some plants certain cells are specialized, forming a more localized sense organ. In either

[23] TRANSEAU, E. N., On the development of palisade tissue and resinous deposits in leaves. Science N. S. **19**:866–867. 1904.

[24] HABERLANDT, G., Die Perception des Lichtreizes durch das Laubblatt. Ber. Deutsch. Bot. Gesells. **22**:105–119. *pl. 8.* 1904.

case the essential feature is a sensitive layer of protoplasm and an apparatus which concentrates the light upon this plasma, of which certain regions are either more or less strongly illuminated when the organ is out of its normal relation to the incident light. Two types are distinguished: those in which the outer face of the epidermal cell is convex, and those in which the inner wall is convex toward the mesophyll or is the frustum of a cone. The hypothesis is not supported by any experimental evidence, but is constructed merely from anatomical observations and *a priori* reasoning. (See also p. 157.)—C. R. B.

WAGER[25] has studied the nucleolus during nuclear division in the root of Phaseolus. After a summary of the extensive literature and a description of methods, the subject is presented under the following heads: the resting nucleus, structure of the nucleolus, changes in the nucleolus during the prophase, and reconstitution of the daughter-nuclei. The main conclusions are that the nucleolus simply forms a part of the nuclear network, in which chromatin or chromatin-substance may be stored, and therefore is not an independent organ of the nucleus; that it is concerned in the formation of the chromosomes, and possibly also in the production of the spindle, and that a portion of it may in some cases be extruded into the cytoplasm and there disappear; that in the reconstruction of the daughter-nuclei the chromosomes unite together in a more or less irregular mass or thick thread, out of which is evolved the nucleolus and nuclear network, the major part of the chromatin passing ultimately into the nucleolus, except in cases where division again immediately takes place. Attention is called to the fact that if these conclusions are correct, the part played by the chromosomes in heredity will need revision, and that the nucleolus as well as the chromosomes will have to be taken into account.—J. M. C.

SALMON[26] has published the results of experiments with the so-called "biologic forms" of the Erysiphaceae, that is, races of individuals morphologically identical, but differing physiologically in possessing distinctive and sharply defined powers of infection. This specialization of parasitism has been found to be associated with both conidia and ascospores. The present experiments show that the restriction in power of infection characteristic of "biologic forms" breaks down if the vitality of the leaf is interfered with in certain ways, as by wounding. It was found also that conidia produced on a wounded leaf that was normally immune to such attack would infect uninjured leaves of the plant in question; by means of this "bridge" passing from one host plant to another. Injuries to leaves in nature, resulting in such bridging, were observed to be made by the "green fly" (Aphis). Therefore, in the evolution of "biologic forms" two sets of factors are at work: one, called "specializing factors," tending to specialize parasitism and deriving from a single morphological species a number

[25] WAGER, HAROLD, The nucleolus and nuclear division in the root apex of Phaseolus. Annals of Botany **18**:29–55. *pl. 5*. 1904.

[26] SALMON, ERNEST S., Cultural experiments with "biologic forms" of the Erysiphaceae. Phil. Trans. Roy. Soc. London B. **197**:107–122. 1904.

of "biologic forms;" the other, called "generalizing factors," bridging these differences and causing "the separate streams of evolving 'biologic forms' to flow into each other." It is thought that these facts may explain the sudden appearance of a parasitic disease on plants which had hitherto proved immune.— J. M. C.

DUVEL[27] has been investigating, since 1899, the causes affecting the vitality of seeds, with special reference to the conditions under which they are stored commercially. The general method pursued has been to store seed experimentally under all sorts of conditions, and afterward to ascertain the exact percentage of germination. The first factors determining the vitality of a seed are maturity, weather conditions at the time of harvesting (damp weather lowering the vitality), and methods of harvesting and curing (especially avoiding excessive heating). The life-period of a seed that has met these favorable conditions depends on environment, but the average life varies greatly in different families, genera, or even species. There is no relation between the longevity of plants and the viable period of the seeds they produce. With proper precautions, the life of seeds may be greatly prolonged beyond the present record, and in commercial handling moisture is the chief factor in shortening it. It seems that seeds can endure any degree of drying without injury, and that such a reduction in the water content is necessary if vitality is to be preserved for a long period of years. It is said that "respiration" is not necessary to the life of a seed, and that the evidence goes to show that it "is not dependent on the preservation of the particular ferment involved or on the zymogenic substance giving rise to the enzyme." "The one important factor governing the longevity of good seed is *dryness*." —J. M. C.

S. M. COULTER[28] has published a preliminary account of his investigation of swamps. The paper is intended to collect and group together the facts concerning the swamp areas investigated as a basis for a future study of the problems involved. The data have been obtained from field studies extending through three years and including swamps of six types: (1) a drained swamp along Crooked River, in the northern part of the lower peninsula of Michigan; (2) an undrained tamarack and black spruce swamp on North Manitou Island, Lake Michigan; (3) a slowly drained arbor vitae swamp on the same island; (4) the small, swampy lakes south of Chicago; (5) Horseshoe Lake, an old "ox-bow" cut off from the Mississippi River in southwestern Illinois; and (6) a cypress and tupelo gum swamp in northeastern Arkansas. The discussion of these types consists of a description of the present topographical condition of each area, together with a summary of the principal plant forms that characterize it. In short, the paper is a brief comparison of certain widely separated swamp areas

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[27] DUVEL, J. W. T., The vitality and germination of seeds, pp. 96. Bull. 58. Bur. Pl. Industry, U. S. Dept. Agric. May 28, 1904.

[28] COULTER, SAMUEL MONDS, An ecological comparison of some typical swamp areas. Rep. Mo. Bot. Gard. **15**:39-71. *pls. 24.* 1904.

of different types expressed in terms of physiography and taxonomy, the history and dynamics of each being reserved for later treatment.    A somewhat detailed account is given of *Nyssa uniflora*, special attention being called to the very much enlarged base, an enlargement which does not become conspicuous where the water supply is scanty; and of *Taxodium distichum* with its enlarged base and "knees," neither of which phenomena appears in connection with dry soil.    The half-tone reproductions of good photographs are excellent and form a substantial addition to the data presented by the paper.—J. M. C.

REGENERATION.—WINKLER'S [29] experiments on Torenia show that detached leaves of this plant may produce buds from any part of the upper epidermis. The shoots proceeding from these buds bloom at once, independent of the age of the parent plant and of the place on the plant from which the leaf is taken. The term "regeneration" should be confined to cases such as this, where fully differentiated cells resume the embryonal state.—SIMON [30] has studied the exact region of regeneration in root tips, and determined by microscopic observation and by experiment that the pericambium is essential.    He distinguishes direct regeneration or replacement of the tip from partial regeneration, where the pericambium grows out from the cut surface in the form of a ring and the new tissue eventually spreads over the whole cut surface.    The latter variety of regeneration occurs when more than about $0.75^{mm}$ of the root tip is cut off; if $1-3^{mm}$ is cut off, no regeneration takes place, but lateral roots replace the primary root.    Three periods of regeneration are distinguished: (1) reaction, time occupying about one day, (2) introductory phase, consisting in pericambial division, (3) definite formation of the new tissue.—VÖCHTING [31] calls attention to the marked lack of plasticity in *Araucaria excelsa*.    The bilateral branches of the first order when used as cuttings produce a plant which retains the bilateral habit; branches of the second order root slowly and grow in length without branching; only the tip of the main axis gives a plant of the regular radial habit.    As to the nature of regeneration in general, the writer holds that the capacity to regenerate, though not always of use either to the individual plant or to the species, is as characteristic a phenomenon as is growth.—M. A. CHRYSLER.

THE MODE in which light affects perceptive organs is awakening interest. In his paper summarized on p. 154, HABERLANDT suggests that perhaps light is perceived by reason of the difference in pressure between illuminated and dark areas.    The same suggestion is made by JOST,[32] but neither mentions RADL,[33]

[29] WINKLER, H., Ueber regenerative Spossbildung auf den Blättern von *Torenia asiatica*.    Ber. Deutsch. Bot. Gesells. **21**:96–107.  1903.

[30] SIMON, S., Untersuchungen über die Regeneration der Wirzelspitze.    Jahrb. Wiss. Bot. **40**:103–143.  1904.

[31] VÖCHTING, H., Ueber die Regeneration der *Araucaria excelsa*.    Jahrb. Wiss. Bot. **40**:144–155.  1904.

[32] Vorlesungen über Pflanzenphysiologie 586.    Jena. 1904.

[33] Unters. über den Phototropismus der Tiere.    Leipzig. 1903.

who seems to have ascribed phototropism in animals to the same fundamental cause, though he thinks of the reactive pull rather than pressure. Utilizing the figures calculated by MAXWELL (1873) and recently determined experimentally by NICHOLS and HULL,[34] the pressure on a cell $.01^{mm}$ square in full sunlight would scarcely amount to $7 \times 10^{-11}$ milligram! To believe that a plant cell could discriminate between o and $.000,000,000,07^{mg}$ pressure (*i. e.*, of darkness and of full sunlight) makes a severe test of one's credulity; but when one remembers that some plants discriminate between darkness and the light of one candle at a distance of $50^m$, and that the phototropic optimum of Vicia lies at 3 candles, the reason simply balks at any possibility of the perception of such differences of pressure.

RADL, who has enunciated this idea regarding phototropism in animals,[33] and who endeavored unsuccessfully to test it experimentally with them, has turned to seedlings for confirmation. In a late paper[35] he endeavors to minimize the objection grounded on the minuteness of the energy involved (which seems absolutely conclusive against the hypothesis), and describes briefly a series of experiments in which he hung seedlings horizontally in a moist chamber by a cocoon filament, so that they were poised at right angles to light admitted through a slit, while control seedlings were fastened in a like position. He then observed whether or not the free ones were caused to rotate, directing their apices toward the light. Arguing that according to the extent of such rotation any curvature they might also attain would be less than in the fixed controls, he interprets his 51 results as giving 39 cases in support of his hypothesis and 12 against it. The sources of error both in experimentation and interpretation are so numerous and the results are so inharmonious as to leave the matter still *in statu quo*. The author recognizes the inconclusiveness of his results, but thinks them suggestive. —C. R. B.

MUCH HAS BEEN written regarding the mycoplasm theory put forth by Dr. JAKOB ERIKSSON, of Sweden, to account for outbreaks of wheat rust when external infection from aecidiospores or uredospores is presumably impossible. In a recent article[36] ERIKSSON gave a concise statement of his position, in order to set right his critics and opponents in regard to the fundamental conception of his theory.

He has now laid the botanical public under a debt of gratitude by publishing a first instalment of his histological studies which form the solid basis of his theory, and by illustrating them with excellent colored plates.[37] Beginning is

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[34] Physical Review **17**: 101. 1903.

[35] RADL, E., Ueber die Anziehung der Organismen durch das Licht. Flora **93**: 167–178. 1904.

[36] Archiv für Botanik **1**: 139–146.

[37] ERIKSSON, J. and TISCHLER, G., Ueber das vegetative Leben der Getreiderostpilze. I. *Puccinia glumarum* in der heranwachsenden Weizenpflanze. Kongl. Svensk. Wet. Akad. Handl. **37**: —. [no. 6. pp. 19.] *pls. 3.* 1904.

made with a study of the vegetative life of the yellow rust of wheat, *Puccinia glumarum*, a species not known outside of Europe, and for which no aecidium has been discovered.

After an introduction, in which some of the difficulties in explaining infection and distribution are indicated that have arisen since DeBary's time, the materials and methods for the investigation are described. Modern histological methods were employed. Best results were obtained with Flemming's fixative, and Flemming's safranin-gentian-violet-orange stain. From October 6 to October 27, 1902, and April 28 to June 18, 1903, no trace of mycelium was found in any of the microtome sections, but in many cells a protoplasmic mixture occurred, which the author has called mycoplasm, because he believes it to be a mixture of the common protoplasm of the cell and the protoplasm of the rust derived from the germinating seed. The mycoplasm does not at first interfere with the chlorophyll grains or nucleus, but these disappear after a time, and the cell wall is filled with a uniform granular mass.

As the wheat plant continues to grow there appears in the intercellular spaces similar granular masses, which soon become filamentous, although possessing no walls or nuclei. As development proceeds, however, well-defined nuclei appear. This naked intercellular stage, whether with or without nuclei, the author designates as protomycelium. This stage is soon followed by the appearance of bounding walls to the filaments, and after a time cross walls, when the ordinary vegetative state of the fungus is attained.

Although the author has not been able to trace the transition between the form within the cells, mycoplasm, and the form between the cells, protomycelium, he is confident that the first gives rise to the second.

Whether or not this clearly stated and well-illustrated article carries conviction to the reader, it nevertheless is a satisfaction to be able so clearly to apprehend the grounds upon which the mycoplasm theory is based.

In a recent article Klebahn[38] has supplemented one of his earlier articles[39] with details bearing directly upon the mycoplasm theory. He gives figures in the text showing essentially the same phenomena which Eriksson has so strikingly set forth with colored plates. The lack of perfect agreement between the two authors can well be ascribed to manipulation of the preparations. But the conclusions drawn from these studies by Klebahn are wholly different from those reached by Eriksson, and favor a theory of abnormal and accidental conditions rather than a theory of mycoplasma.—J. C. Arthur.

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[38] Klebahn, H., Einige Bemerkungen über das Mycel des Gelbrostes und über neueste Phase der Mykoplasma Hypothese. Ber. Deutsch. Bot. Gesells. **22**:255–261. 1904.

[39] Zeits. Pfl. Krank. **10**:88 et seq. 1900.

# ·NEWS·

Dr. Charles J. Chamberlain has been elected a member of the German Botanical Society.

The sixth session of the University of Montana Biological Station is in progress at Flathead Lake, Montana.

Professor Dr. Gy. de Istvánffi has been awarded the Thore prize by the Institut de France for his "Études sur le rot livide de la vigne."

The Bureau of Government Laboratories of the Philippine Islands has undertaken the establishment of a botanical garden at Lamao, across the bay from Manila.

Emmanuel Drake del Castillo died at his Château de Saint-Cyran on May 14, 1904, at the age of 48. He was formerly president of the Botanical Society of France, and a well-known systematist.

Arkiv for Botanik is the title of a new botanical publication, issued by the Royal Swedish Academy of Sciences in Stockholm instead of the Academy's previous "Oefversigt" and "Bihang till Handlingar," which have been discontinued.

Professor Clara E. Cummings, of Wellesley College, has been granted a sabbatical year, which will be spent in resting and studying the tropical flora. Associate Professor Ferguson will have charge of the department for the year.— *Science*.

Dr. Wladislaw Rothert, professor of botany in the University of Odessa, is making a brief tour of the northeastern United States, in connection with a visit to the Louisiana Purchase Exposition. He has had time to see only the botanical establishments at Washington, St. Louis, Chicago, New York, and Boston.

Professor Volney M. Spalding has resigned the headship of the Department of Botany at the University of Michigan. He will continue his work at the Desert Laboratory of the Carnegie Institution at Tucson. All correspondence pertaining to the department should be addressed to Professor F. C. Newcombe.

The Clarendon Press announces that it is preparing to publish translations of Solereder's *Systematic anatomy of the Dicotyledones* by L. A. Boodle and F. E. Fritsch, revised by D. H. Scott; Eichler's *Flower diagrams*, by H. E. F. Garnsey, revised by I. B. Balfour; Knuth's *Pollination of flowers* by Gregg Wilson and Ainsworth Davies; and Warming's *Plant geography*. The translation of the last will be made from a new edition which the author is preparing. It is hoped that the translation will appear simultaneously with the new edition. The name of the translator is not given.

# BOTANICAL GAZETTE

## SEPTEMBER, 1904

## THE DEVELOPMENT OF THE CENTRAL CYLINDER OF ARACEAE AND LILIACEAE.

### CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXII.

MINTIN ASBURY CHRYSLER.

### (WITH PLATES XII–XV)

THE fundamental unity of the vascular structures found in the higher plants was perceived by VAN TIEGHEM, whose conception of the stele and its modifications, outlined in 1886 (**17**), displaced the earlier view of DEBARY. But it became apparent subsequently that VAN TIEGHEM's assumptions were not sufficiently supported by observation. For example, it was shown by GWYNNE-VAUGHAN (**3**) that polystely does not arise by bifurcation of the protostele in the genus Primula, and JEFFREY (**6**) proved the same for *Pteris aquilina*. VAN TIEGHEM's theory is also open to the objection that it is founded on the conditions occurring in a highly organized group of plants, while there would seem to be a better prospect of finding a primitive condition of the vascular system among pteridophytes. In 1897 JEFFREY (**5**) proposed a stelar theory in which this objection is met, the essential feature of which is the important influence on the central cylinder of the outgoing leaf or branch traces. Emphasis is also placed on the study of the young vascular axis, on account of its recognized importance in accordance with the principle of recapitulation. The following diagrams may serve to show the main differences between the two theories:

### I. VanTieghem.

1. Protostele

2. Medullated monostele        4. Polystele

3. Astele (schizostele)        5. Gamostele

II. Jeffrey (using the same numbers to designate equivalent types).

(1) Protostele

(5 and 4) Siphonostele with internal phloem and endodermis (amphiphloic siphonostele)

(3) Siphonostele with internal endodermis (ectophloic siphonostele)

(2) Siphonostele without internal phloem or endodermis.

It will be noticed that Jeffrey derives the vascular structures characteristic of the seed plants from those of the pteridophytes by a process of reduction; further, he considers the pith to be simply fundamental tissue which has intruded through the foliar or ramular gaps, while VanTieghem assumes a stelar origin for the pith.

The researches of Jeffrey (7) and Gwynne-Vaughan (4) seem to place beyond question the view that the ferns possess an amphiphloic siphonostele derived from a protostelic condition by the bending in of phloem, endodermis, and cortex above the point of exit[1] of the foliar traces; but that the seed plants have primitively a central cylinder built on this plan is a generalization which must be tested by the examination of representatives from a number of typical families in different regions of this great group. With this object in view I have undertaken, at the suggestion of Dr. Jeffrey, to investigate the development of the central cylinder in two characteristic monocotyledonous families, the Araceae and the Liliaceae. Such an investigation ought to answer the following questions:

1. What bearing on current stelar theories has the development of the central cylinder in these families?

2. Are the amphivasal bundles found in so many monocotyledons to be considered a primitive type?

[1] For the sake of clearness the leaf traces will be treated as if they originated at the central cylinder, regardless of the actual direction of their development, which in most cases has not been made out.

3. Does the structure of the young stele throw any light on the question of the origin of the monocotyledons?

### ARACEAE.

The number of forms which have been available in this inquiry has not been large, but they are sufficiently varied in their affinities, and appear to the writer to yield no uncertain result.

**Pothoideae.** This subfamily is regarded by ENGLER (**1**) as the most primitive one in the family. Hence one of its most available representatives will be first described.

ACORUS CALAMUS.[2]—In a seedling of this plant the central cylinder in its lowest region is a solid mass of vascular tissue, consisting of a core of xylem and a ring of phloem, surrounded by pericycle and endodermis, that is, it is a typical protostele. One trace is given off to the cotyledon, and usually three traces to each of the next three or four leaves, after which the number of foliar traces is increased. In the region where the traces of the second leaf are given off, the central cylinder is seen to possess a parenchymatous pith, which is continuous with the pericycle through the gaps in the vascular tissues caused by the bending out of the traces (*fig. 1*, which, however, represents a higher region of the stem). The endodermis does not bend inward through the gap with the pericycle, but remains unbroken, a portion of it surrounding the trace as it passes outward. Followed downward through the stele the pith either becomes narrower and disappears above the point of exit of the cotyledonary trace, or in some cases enlarges at this point and communicates with the pericycle at the higher node; followed upward the pith widens out with the enlarging central cylinder. As the three traces of the third leaf bend outward, the pith again communicates with the pericycle; since the median trace is the largest of the three, the gap it leaves in the vascular ring is the widest; in fact, the gap of one or both of the lateral traces may be filled only by a single row of parenchymatous cells or may not be present. Up to this point the vascular ring is practically continuous, owing to the foliar gaps being so short, but in the higher regions of the young stem the gaps remain open longer, so that the central cylinder appears to be made up of a ring of sepa-

[2]The nomenclature employed in this paper is that of Engler and Prantl.

rated bundles which are at first collateral, but soon become amphivasal. *Fig. 1* shows this region of the stele. Not until a considerably older stage is reached do certain bundles turn inward and run for a distance in the medulla before turning out to the leaves. *Fig. 2* shows part of a section through the mature rhizome; most of the bundles are amphivasal, and some of them run in the medulla; *g* is a gap through which a medullary bundle has lately passed, and it will be noticed that the endodermis curves inward around the edges of the gap for a short distance, thus making the cortical parenchyma continuous with that of the medulla. This intercommunication of cortex with medulla is even better marked in the base of the flowering axis, as is shown in *fig. 3*. It will be seen that the endodermis extends around the edges of the gaps for a short distance, and completely encircles one small section of the vascular ring. It seems reasonable to believe that if the gaps in the central cylinder of the seedling of Acorus were not so narrow the cortex might communicate with the pith as it does in the seedlings of other Araceae possessing a wider central cylinder.

ANTHURIUM ACAULE.—In the hypocotyl the central cylinder is a hollow tube consisting of xylem, phloem, pith, and surrounded by an endodermis. Just below exit of the single cotyledonary trace the vascular ring breaks up into a circular row of five or six collateral bundles or meristeles. Above the exit of the cotyledonary trace the row is horseshoe-shaped, but soon becomes circular again owing to the reunion of the bundles on the two sides of the cotyledonary gap. The endodermis cannot be followed clearly owing to its poor development. The stele retains its form of a ring of about six collateral bundles through the first internode. At the upper end of the internode several bundles divide, and certain of these turn outward as traces of the second leaf, while others turn inward and run upward through the pith, becoming traces of leaves higher up. In the young stem no concentric strands have been found.

**Monsteroideae.**—MONSTERA DELICIOSA.—The hypocotyledonary stele consists of a circle of collateral bundles inclosing a parenchymatous medulla. Nearly a third of these bundles bend outward at one side to supply the cotyledon; a little above this point bundles begin to run in the medulla; in other words, the central cylinder early

assumes the characters seen in the adult stem. The bundles are collateral in all parts of the stem. No endodermis can be distinguished.

**Calloideae.**—SYMPLOCARPUS FOETIDUS has already received some attention in JEFFREY's preliminary studies of monocotyledons (**6**). The seedling at the age of one year consists of a spherical tuber about $1^{cm}$ in diameter; from the upper side of this rises a conical bud with a cylindrical base $4^{mm}$ in diameter, from which spring several roots. A transverse section through the basal region of the tuber shows an elliptical row of collateral strands, each surrounded by an endodermis (*fig. 4*). A little higher up several bundles at one side of the ellipse turn outward, so that at about the middle region of the tuber the bundles are arranged as a horseshoe. Opposite the open part of the horseshoe there is frequently a swelling of the tuber, and in some cases this part of the tuber separates off at a slightly higher level by an absciss layer; this part accordingly constitutes the cotyledon, and the opening in the central cylinder is the cotyledonary gap. Toward the upper part of the tuber the separate strands approach one another, as is shown in *fig. 5*.[3] At *g* is the cotyledonary gap; most of the vascular strands have fused laterally, producing a hollow vascular cylinder with an external and internal phloeoterma (using the term in STRASBURGER's sense (**15**, p. 310)), broken by the wide cotyledonary gap and by several areas where the individual bundles have not yet fused; through these openings the external and internal phloeotermas are obviously continuous. The latter may persist for some distance upward, finally becoming indistinguishable, or may degenerate quite early, and, as is seen in *fig. 7*, the external phloeoterma runs for a short distance around the edges of the cotyledonary gap, and then disappears. Compare *figs. 2* and *3* of Acorus, also JEFFREY's figure of *Ranunculus rhomboideus* (**6**, *fig. 16*). A little higher up the cotyledonary gap closes and the stele forms a hollow tube with external and internal phloeoterma. Almost immediately, however, the vascular tissue aggregates into separate strands, the xylem of which is disposed circularly (amphivasal bundles), and a few of these turn into the central region of the stele (*fig. 6*). Each of these bundles is surrounded by a portion of the internal phloeoterma, if this has not

[3] *Figs. 5, 6, 7, 8,* and *11* are from sections treated with sulfuric acid.

already become invisible in this region of the stem, as is seen to be the case in the stem represented in *fig. 8*.   These bundles soon become quite numerous and run upward for some distance before resuming their collateral structure and passing outward to the leaves.

Two points of interest in this plant are the existence of a well-marked internal as well as external phloeoterma in the young stem, and the early disappearance of the internal phloeotermal layer.   It can hardly be doubted that the thin-walled tissue forming the pith of the stele is simply extrastelar tissue which enters at the base of the stelar system, and through the cotyledonary gap.   Absence of the protostelic condition is probably to be accounted for by the shape of the stem; it is in the region of the cotyledonary gap that the central cylinder shows its most primitive condition, namely a vascular tube possessing both external and internal phloeoterma.   The spaces between the vascular segments in the basal region of the stem are not foliar gaps, as JEFFREY's account seems to imply (**6**, p. 29), for this region of the stem is the hypocotyl, and further there are no outgoing bundles between the segments referred to.   Separation of the segments may be due to expansion of the young stem as it assumes its tuberous shape.

CALLA PALUSTRIS has been sufficiently described by JEFFREY (**6**). The development of its stele follows pretty closely the course outlined for Acorus, though the endodermis does not seem to be well developed in Calla, also the foliar gaps extend for a greater distance than is the case in Acorus.

**Philodendroideae.**—SCHIZMATOGLOTTIS ROEBELINII seems to show a scattered disposition of the vascular strands in all parts of its seedling.   The material available has not permitted a satisfactory study.

PELTANDRA VIRGINICA.—The seedling possesses a tuberous base consisting of a somewhat cylindrical axial portion with a thick cotyledon applied to its side; the cotyledon is separated in its upper part from the axial portion by a prominent absciss layer.   In *fig. 9, c* represents the cotyledon, and *r, r* secondary roots.   A section through the basal part of the tuber shows about eight collateral bundles arranged in a circle (*fig. 10*).   Most of these bundles are given off to the cotyledon, so that only a few slender strands continue the

upward course; toward the upper part of the tuber these enlarge and each is seen to be provided with an endodermis whose cells show a cutinized band girdling the radial walls. The strands now unite laterally into a flattened arch whose hollow is turned toward the cotyledon; by continued increase in the vascular tissue the arch becomes more and more nearly a complete circle. In *fig. 11* the cotyledon lies to the right; the individual sheaths have fused to form a common endodermis which is continuous outside and inside the arch; *r* is the trace of a root, which as usual leaves no gap in the central cylinder. *Fig. 12* shows the central cylinder at a slightly higher level; the opening to the right faces the cotyledon, and is undoubtedly the cotyledonary gap. Soon this closes entirely, and at this level the vascular tissue of the stele becomes partly broken up into separate strands, some of which turn into the medulla; each strand and segment of the stele possesses its own endodermis. Amphivasal bundles are found at this level and in the later formed regions of the stem, but they are not so characteristic of Peltandra as of Symplocarpus, to which plant Peltandra evidently possesses many resemblances with respect to its central cylinder. The medullary strands are connected with the traces of all leaves above the cotyledon, and each trace leaves the central cylinder through a gap, around the edges of which the external and internal endodermis are continuous. Eventually, however, the endodermis becomes obsolete, and an increase in the number of medullary strands gives the stele the appearance characteristic of monocotyledons generally. It should be mentioned that the ring of bundles is not always present in the lower part of the tuber; in such cases bundles are so poorly developed in this region that a central cylinder cannot be said to exist below the cotyledonary gap.

Zantedeschia aethiopica (the ordinary calla lily) and Z. albomaculata may be described together, since the seedlings are very similar. As the stele of the root merges into that of the hypocotyl it assumes a pith into which several strands turn from the original vascular ring, and soon the whole stele is converted into a network of anastomosing strands. From this network about six bundles are given off to the cotyledon, whose base forms a sheath around the younger leaves. In the succeeding regions of the stem the bundles

pursue the course ordinarily seen in a monocotyledonous stem. In no part of the stem is an endodermis well developed.

**Colocasioideae.**—ALOCASIA ODORATA.—Above the point of exit of the cotyledonary traces the stele is represented only by a scanty vascular mass of flattened form, its side being turned toward the cotyledon. Further upward this mass splits into several strands, and a ring-shaped row of bundles is completed by the appearance *de novo* of several delicate strands between those already present and the cotyledon. The flattened vascular mass referred to seems to represent the same condition as that shown for Peltandra in *fig. 11*, namely, there is an unusually wide cotyledonary gap, which is not closed in the ordinary way owing to the tendency throughout the plant for the vascular strands to lie widely separated. In a slightly higher region of the stem several bundles come to lie in the medulla and some of the bundles assume the amphivasal shape. No endodermis was found in any part of the stem.

CALADIUM BULBOSUM.—Departure of the cotyledonary trace causes no break in the narrow stele of the seedling; the stele soon becomes complicated by medullary strands which anastomose with one another. In many sections, however, it may be seen that the cortex communicates freely with the medulla above the point of exit of a leaf trace. No endodermis has been demonstrated.

**Aroideae.**—ARUM ITALICUM.—The five traces which pass into the sheathing base of the cotyledon arise from a complex vascular mass, and the succeeding traces run for a short distance in the medulla. The peculiar habits of sprouting described for another member of the genus by RIMBACH (10) and SCOTT and SARGANT (13) have probably had the effect of modifying the vascular system; and no part of the plant suggests a primitive condition, but on the contrary a highly specialized one.

ARISAEMA TRIPHYLLUM.—The method of sprouting is essentially like that of Arum. The five cotyledonary traces rise from a vascular mass whose elements anastomose in a complex manner. Above this region the bundles pursue a more nearly vertical course, but are not arranged in a definite central cylinder surrounded by endodermis. In older seedlings the bundles form an extensive network in the central region of the corm. It is probable that the phylogenetic

development of this corm has been accompanied by considerable changes in the vascular system, leading to complications which render this plant unsuitable for the purposes of the present inquiry.

ARISAEMA DRACONTIUM, A. SPECIOSUM, A. INTERMEDIUM, and A. TARTARINOWII all resemble *A. triphyllum* in having seedlings which show a complex network of bundles. They all likewise produce a corm.

TYPHONIUM DIVARICATUM has a vascular system so similar to that found in Arisaema that it does not merit a separate description.

In viewing in a general way the genera so far described the question arises: What characters are to be regarded as primitive? The answer must be, those which occur in the first formed part of the stem, unless there is reason to believe that this region has been influenced by the assumption of some special habit, such as the tuberous or bulbous habit. The stem of Acorus is relatively free from external influences, on account of its geophilous habit; its central cylinder is at first protostelic, then siphonostelic with a pith communicating with the pericycle through the foliar gaps. Judging from the conditions in Symplocarpus and in the mature organs of Acorus, we may infer that if the central cylinder of the Acorus seedling were not so narrow the endodermis and cortex might here also enter through the gaps, in which case the stele would differ from that characteristic of the ferns mainly in the absence of internal phloem, a feature which appears to be quite rare in seed plants. The simple siphonostelic stage persists in Acorus for several internodes, and the stem looks much like that of a dicotyledon; higher up some segments of the stele become amphivasal, and this may be regarded as the first appearance of a monocotyledonous character; very soon certain strands begin to run in the medulla, and so the monocotyledonous nature of the stele is established. The steles of the various genera differ from the type just described in a modification of the basal part of the stele in accordance with the tuberous habit, as in Symplocarpus, or in the rapid disappearance of the phloeoterma, as in Peltandra, or in the early appearance of the medullary strands, as in Arisaema. Whatever may be the nature of the pith in Acorus, there seems to be good reason for believing that in Peltandra and Symplocarpus the pith is

simply fundamental tissue which has been inclosed by the gradual curving around of the edges of the cotyledonary gap until they meet; moreover, the stele is in open communication with the cortex in the basal region of the tuber.   It has been shown that in Symplocarpus the internal phloeoterma undergoes a more or less early degeneration, so that the included parenchyma comes to lie next to the xylem, and so might be mistaken for stelar tissue in the upper part of the stem.

It is of interest to note that from a general morphological study of Araceae ENGLER (1) places Acorus among the most primitive genera of the family, and members of the Aroideae, such as Arum and Typhonium, among the most highly developed of the family. My observations on the seedlings accord in the main with ENGLER's classification; the young stem of Acorus possesses a simple stele, while members of the Aroideae early acquire the most complicated vascular system found in the family.

## LILIACEAE.

In this family over fifty species have been studied, representing all the large subfamilies; in most cases both the adult plants and seedlings have been examined.   The search for primitive types has convinced me that ancestral characters are most likely to be preserved in a rhizome, since such a stem is free from the modifying influences of an aerial life; hence the first subfamily to be treated is one in which most of the members have the basal portion of the stem a rhizome.

**Asparagoideae.**—CLINTONIA BOREALIS.—The plant is characterized by a horizontal rhizome which turns upward at the end, bears a number of scales and several foliage leaves, and terminates in a scape carrying an umbel of flowers.   *Fig. 13* represents a cross section through the rhizome a short distance before it turns upward; it will be seen that the stele forms a tube perforated at the point of exit of several leaf traces, also that there are no medullary bundles.   *Fig. 14* is a more highly magnified view of a portion of the stele.   It shows that an internal as well as an external phloeoterma is present, and that these are continuous through the foliar gap; also that some of the meristeles are amphivasal.

CLINTONIA UMBELLATA.—A cross section through the rhizome is shown in *fig. 15;* two foliar gaps with their traces are to be seen, and

here also is an internal as well as an external phloeoterma.   Certain
of the strands are amphivasal, and three of these have left the stelar
ring and run immediately adjacent to it in the medulla.   The vascular
system of this plant evidently represents a condition slightly more
complicated than that present in *C. borealis*.   Unfortunately seed-
lings of neither species of Clintonia have been available, so that the
origin of the interesting condition seen in the mature stem remains
unknown.

MAIANTHEMUM BIFOLIUM.—The general habit of the plant is
similar to that described for Clintonia, though the two foliage leaves
arise from a higher region of the aerial shoot.   *Fig. 16* represents a
section through the rhizome a short distance above where it turns
upward.   The heavily cutinized external phloeoterma is a prominent
feature, and inside of it is a circle of collateral bundles; three amphi-
vasal bundles run in the medulla, but these do not become leaf traces;
on the contrary they end as they begin, namely, by joining bundles
of the vascular ring.   Throughout the horizontal course of the rhi-
zome no medullary bundles are present.   Several leaf traces are to be
seen at various stages in their escape from the stele; it will be noticed
that they cause no break in the continuity of the phloeoterma.

In the seedling the stele contains pith even in the hypocotyl; as
the single cotyledonary trace leaves the stele, the phloeoterma bends
inward around the edges of the gap, but does not lose its continuity;
the pericycle is continuous with the pith through the gap and no amphi-
vasal strands are present.   To the second leaf three traces are given
off; the median trace causes the phloeoterma to bend inward, as does
the cotyledonary trace (*fig. 17*); the lateral traces emerge exactly as
in the adult stem (*fig. 16*).   The third leaf receives three traces which
leave the stele as do those of the second leaf; the same is true of the
fourth and fifth leaves.   Comparing the stele of this plant with that
of *Clintonia borealis*, the absence of internal phloeoterma and the
presence of amphivasal medullary strands in the former are to be
noted, though these do not make their appearance until a late stage
of development.

SMILACINA STELLATA.—As the primary root merges into the hypo-
cotyl, the stele becomes hollow and the vascular tissue aggregates in
several collateral strands at the periphery of the stele.   An external

phloeoterma is present and is not broken by the exit of a large strand of vascular tissue to the cotyledon. *Fig. 18* shows the appearance of the stele in the first internode, and illustrates the tendency which the stele has to break up into separate strands. The three traces of the second leaf arise in the same manner as the cotyledonary trace; above this level, however, some of the strands become concentric, and one or two branches are given off into the pith, where they run only a short distance, join bundles of the vascular ring, and then pass out to leaves. *Fig. 19* shows such a strand at *m*, and also a leaf trace (*t*) which is just leaving the vascular ring. Higher up other medullary strands run for a greater distance in the pith and turn outward to leaves without anastomosing with bundles of the vascular ring. The seedling of this plant shows clearly the gradual appearance of mono-cotyledonous characters in a central cylinder which in its first formed part closely resembles that of a dicotyledon. The mature stem both in its subterranean and aerial regions differs from the rhizome of Maianthemum in having a number of medullary strands.

SMILACINA RACEMOSA.—In the youngest plants obtainable the central cylinder exhibited the characters of the adult stem, that is the bundles are scattered through the medulla. Seeds of this plant failed to sprout.

STREPTOPUS ROSEUS.—The stele of the seedling resembles that of *Smilacina stellata* in that it consists of a ring of collateral bundles surrounded by a phloeoterma and enclosing pith; but the bundles early become concentric and afterwards some of them run in the medulla. Bundles of the vascular ring turn outward as leaf traces without destroying the continuity of the phloeoterma.

POLYGONATUM BIFLORUM and P. VERTICILLATUM.—The central cylinder, at first a solid mass, becomes divided into about six widely separated collateral strands at a comparatively young stage; later several medullary bundles appear; a phloeoterma is not distinguish-able. The wide separation of the strands is probably due to the fact that the subterranean stem (a horizontal rhizome) early becomes swollen into ovoid form through deposition of starch.

MEDEOLA VIRGINIANA.—The cotyledonary gap is wide; as this closes the stele becomes divided into six or eight meristeles arranged circularly, each provided with its own endodermis and having a

collateral structure.   The meristeles unite at the next node and a
single strand turns outward, leaving a wide gap in the vascular ring.
Again the meristeles separate widely, owing no doubt to the fleshy
nature of the stem which by this time has begun to show its habit of a
horizontal somewhat swollen rhizome.   As the stem turns upward
into the air the meristeles approach one another and some of them
become amphivasal.   At about this point the internal endodermis
disappears, but the external layer becomes strongly cutinized.   The
amphivasal strands resume their collateral structure at a slightly
higher level; medullary strands are absent in most plants.

TRILLIUM GRANDIFLORUM.—The subterranean stem is a vertical
rhizome which becomes thicker and more ovoidal as the plant grows
older, owing to deposition of stores of starch.   In the young stem
the central cylinder is a solid mass of vascular tissue for a few inter-
nodes.   The first leaves have three traces; the median trace is much
the largest, and as it leaves the central cylinder the latter becomes
somewhat crescent-shaped; the lateral traces are very delicate and
by their departure leave no indentations in the stele.   After exit
of the traces of the third or fourth leaf, however, there is intrusion of
fundamental tissue into the central cylinder, since the angles of the
crescent above referred to curve around and finally close in on the
side next the trace.   This condition is shown in *fig. 20*; *t* is the median
trace, $t_1$ is one of the lateral traces whose gap was narrower than
that of the median trace and had already closed at this level.   The
writer fails to see how the thin-walled tissue inside the stele can be
regarded as anything but a portion of the fundamental tissue inclosed
by approximation of the vascular tissue at the sides of the gap.   The
appearance above described may be masked by the overlapping of
two foliar gaps on opposite sides of the stele; in such a case the stele
is broken into two halves (*fig. 21*), a condition which has frequently
been described for various ferns.   In the upper part of the rhizome
the stele becomes complicated by bridges of vascular tissue reaching
from one side of the stele to the other; also certain of the leaf traces
run for a short distance in the medulla before turning outward.   It
should be remarked that these medullary strands are amphivasal.
In some seedlings the stele retains its solid or protostelic character
for many internodes, and it is possible that the diversity noticed in

the various serial sections of seedlings may be due to some of them belonging to *T. erectum* rather than to *T. grandiflorum*, since the seedlings of the two species are hard to distinguish in the field, and I have been unsuccessful in attempts to grow them from seed. In many instances a leaf trace arises from one side rather than from the base of the gap, as has been observed in many ferns, or the trace may run vertically for some distance before turning out from the stelar ring. This condition is shown by the trace marked $t_1$ in *fig. 22*; $t_2$ and $t_3$ are the lateral traces of the same leaf; the last has not quite broken away from the stele.

TRILLIUM SESSILE and T. RECURVATUM greatly resemble *T. grandiflorum* in the seedling stage, but differ from the last species in having wider gaps and showing concentric bundles in a younger part of the stem.

ASPARAGUS OFFICINALIS, A. VERTICILLATUS, A. SPRENGERI, A. VERTICILLATUS, A. BROUSSONETII, and A. MEDEOLOIDES do not appear to throw any light on the problems under consideration on account of the complications attending the formation of lateral buds.

RUSCUS ACULEATUS has a seedling much resembling those found in the genus Asparagus. In the seedlings available the stele had already assumed its mature condition.

**Dracaenoideae.**—YUCCA FILAMENTOSA.—The hypocotyledonary stele consists of a hollow vascular tube from which about one-third of the vascular tissue turns outward to the cotyledon, leaving a U-shaped stele whose pith is in free communication with the cortex. No phloeoterma was observed. Almost immediately strands turn from the U into the pith, and before the cotyledonary gap is closed these medullary strands are quite numerous. These become traces of higher leaves, so that the stele in this plant quickly attains the characteristic monocotyledonous condition. Nearly all the vascular strands are collateral.

YUCCA ANGUSTIFOLIA and Y. BACCATA resemble *Y. filamentosa* in the young state; in the first-named species the medullary bundles are somewhat later in arising than in the two other species.

DRACAENA DRACO, D. RUBRA, D. VEITCHII, and CORDYLINE AUSTRALIS differ in no essential respect from Yucca as regards the development of the stele.

ASTELIA sp. (*Funkia coerulea*) offers no points of significance.

**Lilioideae.**—LILIUM CANADENSE.—The young plant consists of a vertical axis upon which is set a spiral series of fleshy awl-shaped scales which are loaded with starch; to each of these three traces run from the tubular central cylinder, taking a course directly outward or even curving downward for a short distance after leaving the central cylinder. These traces, though slender, subtend foliar gaps which frequently extend the whole length of an internode, so that the central cylinder has the appearance of three separate collateral strands, except at the nodes, where a vascular ring is formed, and in the lower part of the seedling, where the scales are more crowded. *Fig. 23* shows the appearance of the central cylinder at a node, *t* is the median trace; bordering the vascular strands are cells differing from the surrounding parenchyma by their entire lack of starch; these may represent a phloeoterma. In the higher regions of the stem the usual medullary bundles appear, and some of these are amphivasal.

ERYTHRONIUM AMERICANUM, CALOCHORTUS VENUSTUS, GALTONIA CANDICANS, SCILLA HYACINTHOIDES, CAMASSIA FRASERI, HYACINTHUS CANDICANS, and LACHENALIA PENDULA early assume the bulbous habit characteristic of the adult plant, hence the stem is flattened in the vertical direction. The complications produced in the vascular tissues by this habit render these genera unprofitable for study, and since there is no reason to believe that the bulbous condition is a primitive one, no description of these genera will be necessary here.

**Allioideae.**—ALLIUM CEPA, A. CANADENSIS, and A. ANGULOSUM have seedlings much resembling those of the last group in their bulbous habit and intricate vascular system.

AGAPANTHUS UMBELLATUS has a stele much resembling that of Allium.

**Asphodeloideae.**—ASPHODELUS FISTULOSUS, ASPHODELINE LIBURNICA, BULBINE ANNUA, B. FRUTESCENS, ANTHERICUM LILIAGO, CHLOROPHYTUM ELATUM, KNIPHOFIA TYSONI, K. BREVIFOLIA, and ALOE sp. agree in having short internodes and passing quickly through the early stages of stelar development, so that the medullary bundles are found near the exit of the cotyledonary traces. Further, an endodermis is rarely discernible, so that these genera are unsuitable in the present investigation.

ANEMARRHENA ASPHODELOIDES has been studied with much interest because Miss SARGANT (11, 12) considers that the vascular system of the seedling represents a primitive type. The theory of this author considers chiefly the cotyledonary traces and their insertion; it is natural to inquire whether the stele of the older seedling shows features which may be regarded as primitive. The stele possesses a medulla below the exit of the two cotyledonary traces; these subtend wide gaps through which the cortical and medullary parenchyma freely communicate; the traces of the second leaf are three in number, and before they emerge medullary bundles have made their appearance. Except in the root an endodermis cannot be identified. This fact, and the early appearance of medullary strands, and the presence of a pith in the hypocotyl I do not regard as primitive characters, though it is evident that a plant may retain some ancestral features and lose others, so that the disposition of the cotyledonary strands may still represent an ancestral type.

Melanthoideae.—GLORIOSA SUPERBA.—The peculiar habit of the subterranean portion of the stem has been fully described by QUEVA (9), and sufficiently accounts for the complications found in the lower part of its stele; in the upper internodes of the seedling, however, the vascular strands are arranged in a simple ring, and certain of the strands turn outward as leaf traces after anastomosing with adjacent members of the ring.

UVULARIA GRANDIFLORA.—At the point of departure of the cotyledonary trace a wide gap is left in the vascular tissues; here fundamental tissue enters and extends downward into the hypocotyl for a short distance as well as upward. *Fig. 24* shows the stele at level of the cotyledonary gap; the cotyledonary trace is not visible because it bends downward after leaving the stele; though no distinct phloeoterma is visible, the small-celled tissue surrounding the stele certainly does not seem to be continuous across the gap, as it is in some of the adult stems already described. At one place in the stele it will be noticed that the xylem surrounds a mass of phloem, so that the concentric bundles begin to show themselves at this early stage; they make up the whole vascular ring above the point of exit of the second leaf trace; some of them then turn inward and run in the medulla, but here they soon become collateral.

Viewing in a comparative way the genera of Liliaceae described in the foregoing paragraphs, it appears that Trillium exhibits very clearly the stages in development of the stele. These stages may be briefly enumerated as follows: (1) the protostelic condition is present in the basal part of the stem and persists through one or more internodes; then follows (2) the siphonostelic condition in which cortical tissue is included in the stele above the point of exit of the leaf traces and thenceforth forms a medulla; (3) many segments of the stele take on the amphivasal character; (4) strands of vascular tissue, usually amphivasal, turn into the medulla where they run for a greater or less distance and may become connected with leaf traces. Though the stem of Trillium seldom shows any traces of a phloeoterma, *Clintonia borealis* presents a diagrammatic example of a stele which never gets beyond stage (3), and has external and internal phloeoterma which communicate through the foliar gaps. The internal phloeoterma is probably degenerate in Maianthenum except at the edges of the leaf gaps of the young stele; there may be a physiological correlation between the very heavily cutinized external layer and the absence of an internal layer; stage (4) is much delayed in this plant. In *Smilacina stellata* stages (3) and (4) appear sooner; the phloeoterma is less distinct. Medeola and Lilium show the effect of long internodes combined with extended gaps in breaking up the central cylinder into several strands arranged on the circumference of a circle. Uvularia and Streptopus quickly pass into stage (3). Many members of the family such as Allium have assumed the bulbous habit, and in the very short stem of these plants the medullary strands appear very early. They probably express the highest order of specialization shown in the family.

As to the bearing of the foregoing observations on the central cylinder of the two families upon so-called stelar theories, it may at once be stated that though the pteridophytes must be the critical group in any discussion of these theories, yet information from even so highly specialized a group as the monocotyledons is of importance, if we acknowledge the descent of the seed-plants from fern-like ances-

one considers the adaptations which these plants show; but several plants of both families show characters which, to say the least, are significant.

Concerning VANTIEGHEM's types, the polystele need not be considered, for no monocotyledon has yet been found with internal phloem; the medullated monostele may be present in such forms as Acorus and Smilacina, but the condi.ion may be equally well explained by assuming the degeneration of an internal phloeoterma, deriving this condition from that shown in Clintonia; what may be called an astele or schizostele is probably present in the mature stem of most members of the two families, but in none of the cases examined does t arise by the breaking up of the stele followed by the uniting of the broken ends of the external endodermis on the inner side of the meristeles; on the contrary, wherever the endodermis is discernible in the region of splitting up of the stele, there is an internal as well as external endodermis which communicate at the leaf gaps (*e. g.*, Clintonia); in Symplocarpus each strand which turns into the medulla is surrounded by a portion of the internal endodermis.

Turning to the theory of JEFFREY, a consideration of the figures which accompany this paper shows that there is evidence in the case of the two families studied to support his fundamental statement that the siphonostelic type of central cylinder "is primitively a fibrovascular tube with foliar lacunae opposite the points of exit of the leaf traces" (6, p. 38). That the simple tubular condition is found for only a few internodes in most cases is due to the monocotyledons having acquired a new mode of insertion of the leaf traces, which has replaced the mode characteristic of ferns. However, in rhizomes, whose subterranean position has shielded them from the disturbing effects of aerial life, a more primitive type of stele is frequently found; seedlings almost universally show a gap in the central cylinder above the point of exit of the cotyledonary trace, unless indeed they are protostelic at this level, as in Trillium. The siphonostelic nature of the central cylinder is often retained for several internodes, but sooner or later the medullary strands appear, or the gaps per through an entire internode, in either case resulting in the the essentially tubular nature of the stele. Th cylinder of so highly organized a group a

te characters is a fact of considerable phylogenetic sig-
nificance evidence concerning the extrastelar or intrastelar
pith is not so plain, but from the method of closure of
the mary gap in Peltandra and Symplocarpus and of the foliar
illium, I am led to believe that the tissue in question has
ded; the hypocotyledonary region in Peltandra and Sym-
also suggests the unity of extrastelar and intrastelar tissues.
s of the gaps would account for the failure of the endoder-
rtical tissue to enter through the foliar gaps in Acorus,
sence of internal endodermis in such plants as Maianthe-
be ascribed to degeneration of such a layer as is found in
part of the stele in Symplocarpus but disappears in the
gions of its stele. Thus it appears that the terms "cortex"
h" should be used only in a topographical sense, and not as
a difference of origin, for morphologically they must be
o as identical, as regions of the "fundamental tissue," using
in the sense of SACHS and DEBARY. Hence if the term
s used, it should be restricted to the vascular elements of the
ylinder, as is insisted on by FARMER and HILL (**2**). Further,
arches of SCHOUTE (**14**) have shown that HANSTEIN's derma-
periblem, and plerome do not correspond to VANTIEGHEM's
is, cortex, and stele, so that there no longer appears to be
ecessity for postulating a common origin for all the tissues found
the endodermal ring. On the whole, then, the development of
ele in the two families in question appears to support the gener-
ons made by JEFFREY.

MEDULLARY BUNDLES.—The writer is inclined to believe that
did not originate as leaf traces, but as strands to which leaf
subsequently became attached. This tentative view rests upon
following considerations:

The tendency of the monocotyledonous stele to break up into
ments makes it easy for a strand to leave its vertical course at the
phery of the stele and run for a distance in the medulla; such a
nd may at a higher level return to its original course, or may join
stelar ring at the opposite side. Both of these conditions are to
een in the young stele of *Smilacina stellata*. In Maianthemum
first medull strands to appear do not come in contact with the
the

leaf traces which arise in this region (*fig. 16*), but high
to the stelar ring. It is probable that the anastomosing
in Trillium, Zantedeschia, etc., are of the same nature.

2. VANTIEGHEM (**16**, p. 172) has shown that in *Acorus*
after a bundle has run for a distance in the medulla it
part bending outward as a leaf trace, the other pursuing the
course, again dividing further on, and finally passing out.
The bundle marked *b* in *fig. 2* is in process of division into a
bundle and a leaf trace.

3. Medullary bundles are either absent or few in num
zomes, but become numerous as soon as the stem turns up
the air; this is not altogether due to the greater development
in the aerial part.

It is probable that these strands have an important m
function, which may explain their paucity in rhizomes;
hardly have arisen in consequence of a crowding out into the
of the too numerous vascular elements of the stelar ring,
occur in stems whose meristeles do not form a complete ri
*Smilacina stellata* (*fig. 19*).

AMPHIVASAL BUNDLES. The mode of formation of th
observed by VANTIEGHEM in the mature stem of *Acorus gra*
(**16**, p. 171); I have traced their formation in the young stele of
*calamus* and *Smilacina stellata*. Starting with a simple co
bundle of the vascular ring it may be seen that the tracheids in
in number so as to give the xylem a U form and finally an O
Some strands never go any further than the U stage, and som
have become concentric lose the tracheids of their outer side.
plain, then, that amphivasal bundles are derived from collateral
and are simply a modification of the latter type. Since phyloge
significance has been attached to the concentric and mesarch bu
found in the petioles and peduncles of cycads, it has been the
worth while to find in what parts of the plant in the Araceae
Liliaceae the amphivasal bundles occur. The result of a some
extensive investigation of this point may be briefly stated as foll
(1) only collateral strands are found in the lowest part of the ste
the seedling; (2) amphivasal strands are found in the older ster
nearly every genus; (3) the floral axes show only collateral stra

be arranged in a circle or scattered; (4) only collateral
found in the leaves. Hence amphivasal strands are to
. as cenogenetic structures.

ervations recorded in this paper seem strongly to support
nt made by JEFFREY (8) that neither the medullary course
dles nor their amphivasal nature are primitive features,
1ey appear at a more or less late stage, and that they serve
uish monocotyledons from other groups. The plan of the
le, *e. g.*, Smilacina, bears a close resemblance to that of a
on, and differs from the older stele of a dicotyledon only in
ce of cambium. The resemblance between the two groups
shown by the occurrence of medullary strands in several
onous families, *e. g.*, Nymphaeaceae, and in the older sub-
stem of *Ranunculus acris* (6, p. 20); also by the occurrence
ivasal strands in the mature tissues of such plants as Rheum
mpanula. These considerations lead to the conclusion that
1ocotyledons are not an ancient group, but that they have
d off from the dicotyledons, or that both groups have sprung
parent stock which resembled the modern dicotyledons more
than it did the monocotyledons.

### CONCLUSIONS.

1. The members of the Araceae and Liliaceae have primitively a
collateral tubular central cylinder, or ectophloic siphonostele, derived
from a protostele, and interrupted by gaps above the points of exit
of the foliar traces; through these gaps the external and internal
phloeotermas communicate; the intrastelar parenchyma is to be
regarded as having the same origin as the cortex, *i. e.*, both cortex
and medulla are portions of the fundamental or ground tissue.

2. This primitive condition becomes altered (1) by degeneration
of either the internal phloeoterma or both the internal and external
phlceotermas; (2) by the assumption of a medullary course by some
vascular strands, with which leaf traces are connected; hence the
scattered arrangement of bundles is to be regarded as a cenogenetic
character.

3. The amphivasal concentric strands are not a palingenetic
feature, for they are derived from collateral strands and do not occur
in the base of the seedling nor in the leaves and floral axes.

4. Anatomical evidence favors the derivation of mon
from dictoyledonous ancestors.

The subject of this paper was suggested by Dr. E. C.
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seeds of various species from the botanical gardens un
direction.

THE UNIVERSITY OF CHICAGO.

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## EXPLANATION OF PLATES XII–XV.

### PLATE XII.

FIG. 1. *Acorus Calamus;* section through stele at point of exit of traces of third leaf. × 90.

FIG. 2. Same; part of mature stem: *b*, bundle in process of division into leaf trace and medullary bundle; *g*, gap through which a leaf trace has recently passed; *c*, cortex; *m*, medulla. × 55.

FIG. 3. Same; central cylinder from base of flowering axis. × 35.

FIG. 4. *Symplocarpus foetidus*; section through basal region of tuber. × 15.

FIG. 5. Same at region of the cotyledonary gap (*g*). × 25.

FIG. 6. Same a short distance higher up; cotyledonary gap closed. × 25.

### PLATE XIII.

FIG. 7. *Symplocarpus foetidus;* specimen showing early degeneration of internal phloeoterma. × 25.

FIG. 8. Same; region above closure of the cotyledonary gap. × 25.

FIG. 9. *Peltandra virginica;* general view showing cotyledon (*c*) partly separated off; *r, r*, secondary roots. × 7.5.

FIG. 10. Same; basal region of seedling. × 30.

FIG. 11. Same; region of cotyledonary gap; *r*, secondary root. × 25.

FIG. 12. Same; cotyledonary gap closing. × 25.

### PLATE XIV.

FIG. 13. *Clintonia borealis;* stele of mature rhizome. × 25.

FIG. 14. Part of section shown in *fig. 13.* × 85.

FIG. 15. *Clintonia umbellata;* stele of mature rhizome. × 20.

FIG. 16. *Maianthemum bifolium;* stele of mature rhizome shortly above region at which it turns upwards. × 25.

FIG. 17. Same at the second node. × 85.

FIG. 18. *Smilacina stellata;* stele in the second internode. × 125.

### PLATE XV.

FIG. 19. *Smilacina stellata;* higher region of seedling; *m*, bundle which has left periphery of stele to run for a distance in the medulla; *t*, leaf trace. × 65.

FIG. 20. *Trillium grandiflorum;* young stele: $t$, median trace of a leaf; $t_1$, lateral trace of same leaf. $\times$ 30.
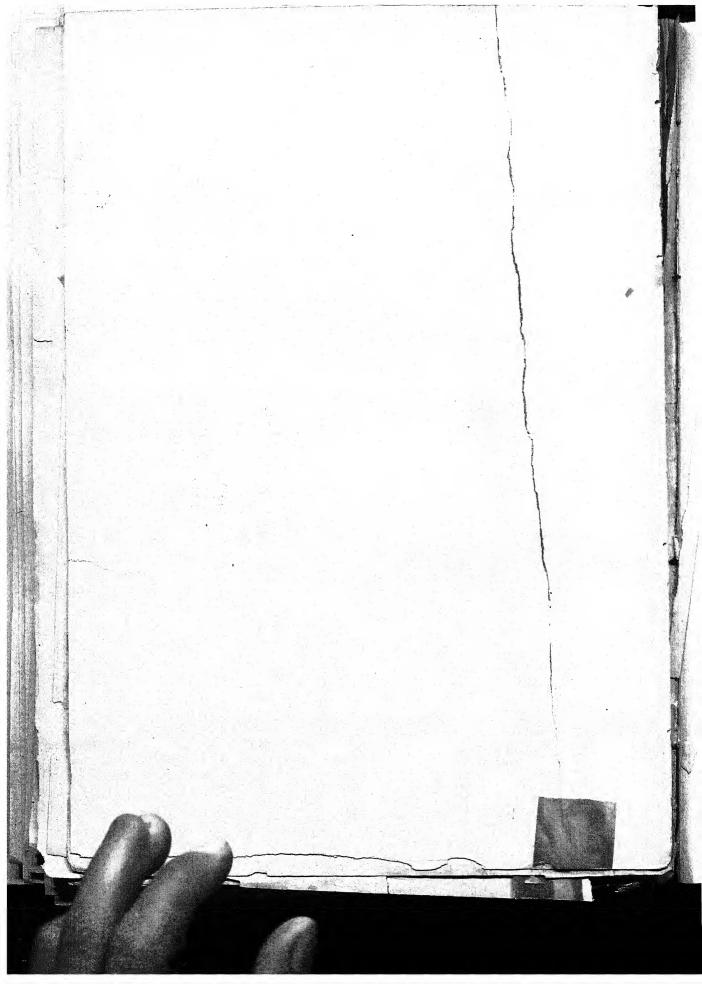
FIG. 21. Same; stele slightly higher than the preceding, showing two foliar gaps overlapping. $\times$ 50.
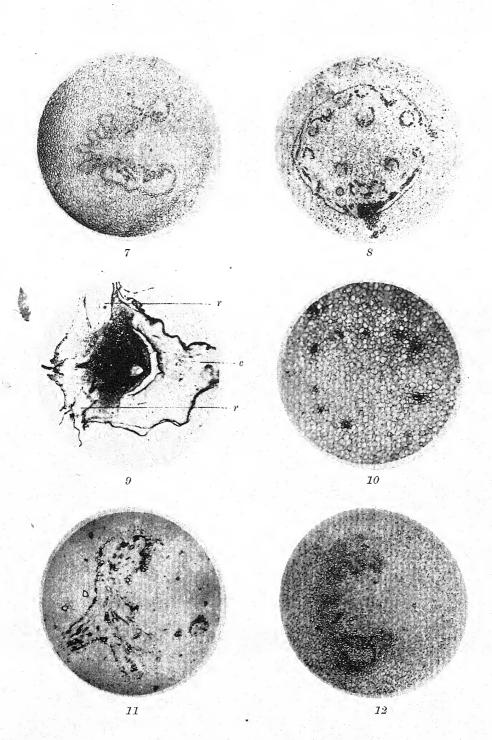
FIG. 22. Same still higher; $t_1$, median trace; $t_2$, $t_3$, lateral traces. $\times$ 50.
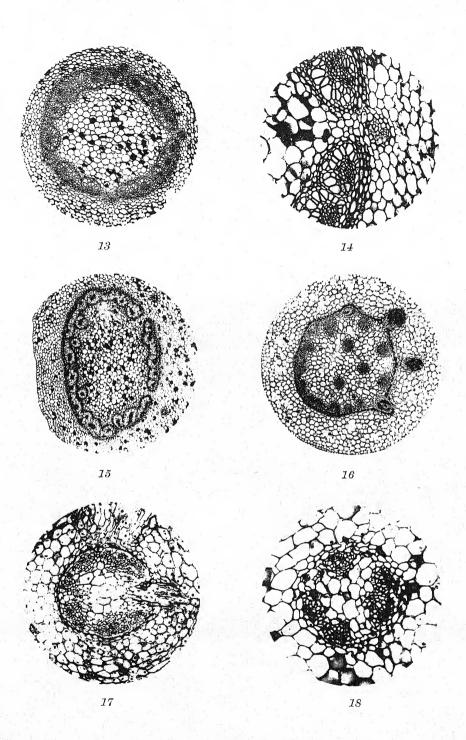
FIG. 23. *Lilium canadense;* node of seedling; $t$, median trace of leaf lying to the right. $\times$ 60.

FIG. 24. *Uvularia grandiflora* immediately above point of exit of the cotyledonary trace. $\times$ 95.

PLATE XII
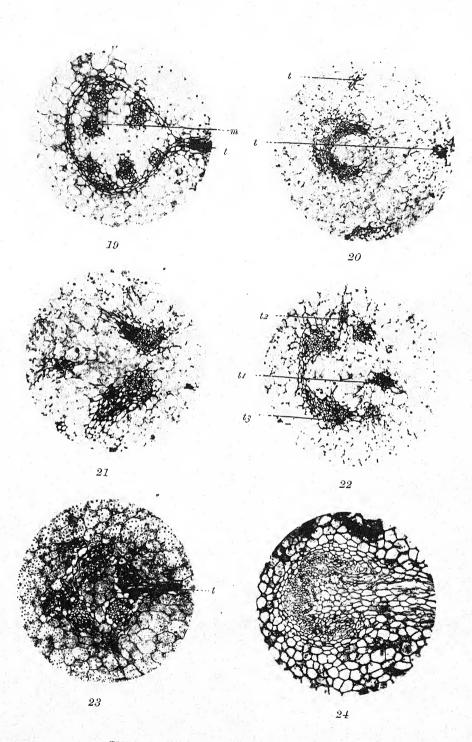
CHRYSLER on CENTRAL CYLINDER.

CHRYSLER on CENTRAL CYLINDER.

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CHRYSLER on CENTRAL CYLINDER.

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CHRYSLER on CENTRAL CYLINDER.

# THE DEVELOPMENT AND RELATIONSHIP OF MONOCLEA.[1]

DUNCAN S. JOHNSON.

(WITH PLATES XVI AND XVII)

WHILE studying and collecting the native Piperaceae of Jamaica, in the spring of 1903, I also preserved plants in various stages of development of the liverwort *Monoclea Forsteri* Hook. The results of the study of the material of this little known form are given in the following pages.

Monoclea occurs in Jamaica chiefly on wet rocks and banks in the mountain forests (CAMPBELL '98). The most luxuriant growth of it seen by the writer was one of many meters in extent in a small depression near New Haven Gap in the Blue Mountains. This depression was filled up considerably by living and decaying vegetation, but the water in it stood at such a level that the tangles of Monoclea and associated plants were practically floating upon its surface. The appearance of a mat of Monoclea is not so much like one of the more attenuated plants of Marchantia or Fegatella as it is like a mat of gigantic Pellia, though the edges of the thallus are often more crisped or curled upward than in the latter genus. The plants growing in the water at New Haven Gap were often 3$^{cm}$ wide, in the case of the broader branches, while elsewhere they seldom exceeded 2$^{cm}$. The growing ends of these aquatic plants were almost erect, apparently because of the wet substratum, since this peculiarity did not seem to be attributable to the direction from which light reached them.

A majority of the plants found were sterile, and in the case of the plants growing in wetter situations fertile plants were very scarce. In groups of plants growing in the damp ravines, where the substratum was not so completely saturated with water, though the air was saturated with water vapor, fertile plants of both sexes were easily found.

The older female plants were most readily distinguishable by the presence of the large tubular involucre enclosing the large sporogonia. Male plants were readily found, being slightly smaller than the female plants, but in most of them the antheridia had matured and discharged, and only the shriveled male receptacle remained. Careful sorting of large amounts of material was necessary at the season I was in Jamaica, in order to discover young male receptacles with developing antheridia in them.

## HISTORICAL RÉSUMÉ.

*Monoclea Forsteri* was originally described by HOOKER ('20), from material collected (in "Insulae Australes") by FORSTER while accompanying Captain COOK on his famous voyage. HOOKER was aided also by a drawing and a manuscript description of the plant by FORSTER, who had named it *Anthoceros univalvis*. The general form of the non-costate thallus, the simple involucre, the lack of a female receptacle, and the structure of the open capsule, all features which were shown in HOOKER's *fig. 1.* were apparently taken from FORSTER's drawing. By study of the specimens HOOKER made out that the unopened capsule was cylindrical, and that it opened by a single lateral slit. He also figured the spores and elaters and noted the presence of three well-developed capsules in a single involucre, each with its own tubular calyptra.

The removal of the plant from the genus Anthoceros, and the establishment of the genus Monoclea to receive it, was based by HOOKER on the absence of the columella and the presence of but one valve in the open capsule.

Ten years later HOOKER ('30) described as *Monoclea crispata* a liverwort found in the island of St. Vincent, in which he found a univalve capsule like that of Monoclea, and a columella like that of Anthoceros. This latter led him to think that he had probably overlooked a columella in *M. Forsteri*, and to decide that Monoclea was probably intermediate between Anthoceros and the Jungermanniaceae.

TAYLOR ('44, '45), apparently after consulting HOOKER's later paper only, added two other species to the genus Monoclea.

A year later NEES VON ESENBECK ('46) established the genus Dendroceros to contain HOOKER's *M. crispata* and Taylor's species,

but failed to recognize the full importance of the differences between the involucre, calyptra, and sporogonium of *M. crispata* and those of the other forms included in the genus by HOOKER and TAYLOR, and apparently based the division of the genus chiefly on the columella.

GOTTSCHE ('58) studied material of Monoclea from Chili. From this he described the gross and minute structure of the vegetative thallus, noting the presence of two types of (non-tuberculate) rhizoids and the occurrence of fungus hyphae in certain cells of the thallus. The involucre he thought completely closed at first. He also described the structure of the mature sporogonium, from the foot to the capsule, with its one-layered wall, unicellular elaters, and roughened spores. On the basis of these observations GOTTSCHE clearly distinguishes *M. Forsteri* from the species of Dendroceros with which it had been associated by HOOKER, TAYLOR, and NEES, and seems to find in it close resemblances to Pellia and Blasia, with which he frequently compares it. He also remarks on the outward likeness to Marchantia which had been noted earlier by HOOKER ('20, p. 176).

Nine years later still GOTTSCHE ('67) discovered the elevated, oval male receptacle on plants of Monoclea from Mexico.

The next important worker on the genus was LEITGEB ('77), who confirmed the work of Gottsche on the structure of the thallus, calyptra and capsule, and insisted on the similarity in structure and branching of the thallus with that of Pellia and Symphyogyna, rather than with that of the dichotomous, areolate Marchantiaceae. He described the slender, thick-walled rhizoids, found by GOTTSCHE ('58), as generally distributed over the under side of the thallus, and as lying parallel to it, while the larger, thin-walled ones are, as GOTTSCHE showed, confined to the median portion of the thallus and stand out perpendicular to the latter. LEITGEB found that the involucre arises as a depression in the tip of the thallus, being closely like that of Pellia in origin and structure. He also discovered that the involucre is independent in its development of that of the sporogonium, and even of fertilization. No young archegonia or embryos were found. The mature archegonia occur in groups of eight or ten, have a large venter, and a long twisted neck. The capsule he thinks imperfectly four-valved. From these facts LEITGEB concludes that Monoclea is more closely related to Pellia than to any of the Marchantiaceae.

In 1881 LEITGEB studied alcoholic material of male and female plants of a Monoclea from New Zealand, the male plants of which had earlier been described as *Dumortiera dilatata*, and found that, except in the larger size of the plants and of the involucre, they agreed closely with *Monoclea Forsteri*. In the male plants he found that the form and distribution of the male receptacles was as described by GOTTSCHE ('67). The receptacles he likens to those of Fegatella, and notes that the elongated, conical antheridia are secondarily sunken in the cavities of the receptacle. These characters of the male plant he thinks show as striking a resemblance to the Marchantiaceae as do those of the female plant to the Jungermanniaceae, but which set of characters is to preponderate as an index of relationship LEITGEB does not definitely decide.

SCHIFFNER('93), in characterizing the genus Monoclea, apparently overlooks the later papers of both GOTTSCHE and LEITGEB, and states that the male plant is unknown. He also says that the wall of the capsule is of two layers of cells, though both GOTTSCHE and LEITGEB say it is one-layered. SCHIFFNER is then naturally led to follow LEITGEB's earlier conclusion ('77) that Monoclea is shown by the female plant and sporogonium to be closely related to Pellia.

Coincidently with SCHIFFNER's work appeared a paper by RUGE ('93), in which he described the development of the male receptacle and the antheridium, as worked out on preserved material from Venezuela, more completely than had been done by LEITGEB. According to RUGE several transverse walls appear in the primarily superficial antheridium mother-cell before any longitudinal ones are formed. The series of figures given does not show the details of the further development of the antheridium clearly, and the series for the archegonium is still less satisfactory.

In this description of the female plant RUGE agrees with GOTTSCHE and LEITGEB, but gives more details as to the development of the archegonial cavity. RUGE, for some reason not clear to the writer, described the slender rhizoids as being also thin-walled and the larger ones as thick-walled, the exact contrary of the condition found by GOTTSCHE, LEITGEB, and the present writer.

CAMPBELL ('98) in a short paper reviews briefly the bearing of the work of HOOKER, GOTTSCHE, LEITGEB, and RUGE, and points out

that the work of the latter (though RUGE apparently failed to appreciate this) materially adds to the likenesses between Monoclea and the Marchantiaceae, which LEITGEB ('81) had already noted.

✓From the presence of two types of rhizoids, the development of the male receptacle and the antheridium, and from the structure of the mature archegonium made out by CAMPBELL himself, he concludes that Monoclea is to be included in the Marchantiaceae. The absence of ventral scales and of the air chambers, characteristic of the Marchantiaceae, he thinks cannot be considered a greater objection here than in the case of Dumortiera, in certain species of which he has shown that the air chambers are not present at any stage of development.

### THE MALE RECEPTACLE.

The male receptacle of Monoclea is a slightly elevated oval area, $4-10^{mm}$ long and $2-3^{mm}$ broad, on the median line of the upper surface of the thallus (*fig. 1*). ✓ In general appearance it is something like the male receptacle of Fegatella, but in origin it resembles more closely that of Fimbriaria (CAMPBELL '95), since the receptacle is not sunken into the thallus and is not the product of several growing points, both of which features CAVERS ('04) has shown to be characteristic of Fegatella.

The antheridia of Monoclea occur in groups of fifteen to fifty, arranged in four to six rather indefinite longitudinal rows along the receptacle (*figs. 1, 2, 4, 6*). They arise in acropetal succession, and the antheridia of the same receptacle may range in development from those of a few cells each at the anterior end to nearly ripe antheridia at the posterior end (*figs. 8, 9*).

The male receptacle arises by the upward growth of the cells of the thallus round about and among the antheridia of a group (*figs. 6, 9*). This upward growth of the sterile cells is subsequent to the formation of the antheridium rudiments (*fig. 6*), and thus progresses, like the development of the latter, from behind toward the growing point. When the formation of antheridia ceases for a time, the growing point which has given rise to the antheridia pushes on, forming a stretch of vegetative thallus of normal thickness (*fig. 9*). Thus the receptacle has an abrupt ending in front, with an elevated and slightly overhanging margin, like that on the lateral and posterior edges (*figs. 2, 3, 8, 9*).

Three or four successive series of receptacles may often be seen on the same plant (*figs. 1, 3*). The youngest of these appear as crescentic regions at the growing point, with only the posterior edge slightly elevated above the thallus (*figs. 1, 4*). Whether more than one series of receptacles arise in one year was not made out with certainty, but I am inclined to believe that one series may be formed in each of the two rainy seasons that occur in Jamaica each year. Not infrequently a receptacle is found which extends up each branch from the point of forking of the thallus. This is due to the division of the growing point into two after the formation of antheridia has begun. The series of antheridia from the two growing points are clearly distinguishable in the young receptacle (*fig. 5*).

The older receptacles, after the ripening and discharge of their antheridia, become somewhat shriveled and brown, but finally disappear only with the progressive decay of the plant from the base (*figs. 1, 3*).

### THE ANTHERIDIUM.

The mother-cell of the antheridium is first distinguishable when it is but a few cells back from the initial of the thallus, but the exact age or portion of the segment from which it arises was not determined. It is first recognizable because of its greater size and the darker staining of its contents, by its failure to divide by perclinal walls as early as the surrounding cells, and finally by the gradual separation of its lateral walls from those of the surrounding cells (*fig. 6*). This separation of the lateral cell-walls begins at the outer surface, and even before it is completed the surrounding cells begin to push upward more rapidly than the antheridium itself, and soon close in above it to a narrow pore (*figs. 6, 8, 9, 13*). Thus each antheridium finally comes to lie in a long-necked, flask-like cavity in the male receptacle. From the cells lining this cavity, club-shaped unicellular hairs are formed, which probably secrete the abundant slime that completely fills the older cavities around the antheridium and oozes out at the neck of the cavity (*figs. 8, 9, 13*). In paraffin sections this slime, with the imbedded hairs, has the appearance of a shrunken cellular jacket. The similar mass of slime in the archegonial cavity led GOTTSCHE ('58, *fig. 16*) to describe this mass as a structureless membrane, bearing hairs.

Soon after the separation of the antheridium mother-cell from the surrounding cells, it divides transversely into a terminal or body cell and a basal or stalk cell. The latter remains attached to the cells at the bottom of the pit, while the former is free from all but the stalk cell (*figs. 6, 10, 13*). The body cell soon becomes remarkable because of its denser contents and its more active division. It first divides twice transversely, and thus gives rise to four primary cells in the body of the antheridium (*figs. 6, 10*). Meantime the stalk cell of the antheridium divides into two, the upper one of which usually remains undivided for some time, while the lower one soon divides by a transverse wall (*figs. 11, 12, 13*). There are thus usually seven tiers of cells in the antheridium at this stage. Of these the three basal ones are concerned with the formation of the stalk, while the four terminal ones give rise to the body of the antheridium (*figs. 11, 12, 13*).

The stalk is more evident in the younger antheridium, since in the older ones, though it is several cells broad, it is usually crushed down by the rapid elongation of the antheridium, which pushes upward against the roof of the antheridial cavity and downward upon the stalk (*figs. 9, 13*).

The first longitudinal wall in each of the four cells of the body of the antheridium is a diametric one (*fig. 15*). Each of the two cells so formed is then cut by a radial, longitudinal anticline, and thus quadrants are formed (*fig. 16*). The next wall appearing in each quadrant is a pericline, which cuts off an outer wall cell from an inner spermatogenous one (*figs. 11, 13, 17*). Next there appears in each wall cell a radial anticline (*fig. 17*), and this is soon followed by other longitudinal and some transverse anticlines, but no periclines are formed in the wall cells except at the tip of the antheridium. Here the cells of a small group divide by one or two periclines, and thus give rise to the thickened terminal area in the wall of the mature antheridium (*figs. 9, 14*). The rest of the wall of the mature antheridium is one-layered throughout. The cells of the wall at maturity are somewhat elongated longitudinally to the antheridium and are about equally thickened on all sides. The place and mechanism of the opening of the antheridium were not observed.

The primary spermatogenous cell of each quadrant of the antheridium breaks up, at first in a pretty regular manner, by approximately

longitudinal anticlines (*figs. 18, 19, 20*).   Then by the appearance
of other longitudinal and transverse anticlines a very large number
of spermatogenous cells are formed.   The nuclear divisions in these
spermatogenous cells occur simultaneously over larger or smaller
blocks, commonly extending over one-tenth to one-fifth the area of
a longitudinal section of the antheridium, but never over the whole
of it at once.   In several of the antheridia examined there were found
to be from 35 to 50 of these cubical spermatogenous cells on a single
diameter, and from 125 to 160 of them in the length of the antheridium.
This means that there are from 100,000 to 250,000 of these cells in a
well-developed antheridium.   Each of these cubical cells divides
later by a diagonal wall to form two triangular-prismatic sperma-
tozoid mother-cells.   There are thus formed from 200,000 to 500,000
spermatozoids in each antheridium.

The organization of the spermatozoid in the mother-cell begins,
as in other described liverworts, by the elongation and coiling of the
nucleus.   The presence of a blepharoplast was not demonstrated.
When mature the spermatozoid is coiled to about one and a half turns
in a flat spiral, whose axis is perpendicular to the broader side of the
triangular-prismatic mother-cell.

The most striking peculiarity shown in the development of the
spermatozoid is the fact that the individuality of the chromosomes
is visibly persistent in the ripe spermatozoid.   Careful study of the
mitotic figures in spermatogenous cells at various stages of develop-
ment showed the number of chromosomes to be eight or ten.   In
preparations of ripe antheridia, which had been fixed in Flemming's
solution and stained in Flemming's triple stain, when washed so as to
show well the chromatin in the vegetative nuclei round about, the
spermatozoids appeared as single dark blue coils.   When however
the sections were washed out more completely, so that even the nuclei
were of a faint blue, the color remaining in the spermatozoid was con-
fined to a number of fine threads of nearly the length of the sperma-
tozoid.   These threads were twisted about each other slightly so that
each thread in its length made a complete turn about the nearly
cylindrical spermatozoid (*fig. 8a*).   A careful count of these threads,
which could best be made in optical transverse sections of the coils
of the spermatozoid, showed that the number is constant and identical

with that of the chromosomes in the spermatogenous cells (*fig. 8b*). The fact that no other part of the spermatozoid retained the stain, and the constant agreement in number just mentioned, seems to leave no doubt that these threads in the spermatozoid are the greatly elongated chromosomes. The significance of this unique individuality of the chromosomes in the nearly ripe spermatozoid might be discovered by a study of the process of fertilization and the behavior of these chromosomes in the fusion nucleus of the fertilized egg. This I was unable to accomplish because of a lack of material of the particular stage needed.

### THE ARCHEGONIUM.

The portion of the thallus from which the archegonia develop is not as much differentiated from the vegetative part as is the male receptacle. The archegonia arise in acropetal succession, in groups of six to ten, on the upper surface of the thallus just back of the growing point. At about the time of origin of the first archegonia of a group, for these differ considerably in age, the thallus begins to thicken just behind the growing point. A longitudinal section of this region at this time would look much like that of a young male receptacle (*figs. 26, 27*). Soon the upper anterior edge of this thickening grows forward to form a hood-like involucre above the archegonia (*fig. 28*). This hood-like roof above the archegonia keeps pace with the advance of the growing point below, and thus is formed the long, tubular involucre, which may become $15^{mm}$ or more in length, though seldom more than $3$–$4^{mm}$ in width (*figs. 22, 29, 30, 31*). Though widely open at first the involucre is finally closed anteriorly except for a very narrow slit, the edges of which fit together closely (*figs. 22, 29, 31*). After a growing point has given rise to a single series of archegonia and has done its part in forming the lower side of the involucre its activity ceases. Then a new growing point appears on each side of the involucre at the anterior end (*fig. 22*). By the activity of these a new branch is formed on each side and the involucre is left behind at the juncture of these two branches.

Lining the walls of the involucre on the inner side, among the archegonia, are large numbers of glandular hairs, which are outgrowths of the superficial cells. These are usually cut off by a transverse wall from the parent cell (*figs. 28, 33*). These slime-secreting hairs

seem, like those of the antheridial cavity, constantly more slender in form than the bent, club-shaped hairs which occur close to the growing point, as was noted by RUGE ('95).

The early stages of the archegonium were not made out as completely as were those of the antheridium, but the stages seen were sufficient to show that the archegonia of Monoclea agree essentially in the early stages of their development with those of other liverworts that have been carefully studied. Thus in *fig. 32* we have a young archegonium with wall cells, a cover cell, and three axial cells of which the lower is evidently destined to form the egg and ventral canal cell, while the upper are to break up into neck canal cells. The structure is in other words identical in all respects with that of the young archegonium of all the well-known Marchantiaceae and Jungermanniaceae (*cf.* CAMPBELL '95, *figs. 2, 17, 46*, and GOEBEL '98, *fig. 137*).

The mature archegonium (*fig. 33*) has a rather broad stalk, a well-marked venter, and, as noted by LEITGEB ('77, p. 67) and RUGE ('93), has also a very long neck (*figs. 28, 29, 33*). In the cavity of the archegonium is found a large, oval egg, a small ventral canal cell, and an unusually large number of neck canal cells. The number of the latter is larger than ten, and in the case figured was apparently fourteen, though the cells shown in dotted outline could not be made out clearly, being located just at the level of juncture of the two adjoining sections from which the drawing was made.

The number of cells seen in a transverse section of the neck of the archegonium is usually six, as shown by CAMPBELL ('98), but occasionally five and frequently seven or eight were found (*figs. 35, 34*).

The twisting of the cells of the neck of the archegonium was not nearly so marked in my material as in that studied by LEITGEB ('77) and RUGE ('93).

As noted above, the hood-like involucre begins its development long before the archegonia are mature, hence, as was pointed out by LEITGEB ('77), it cannot be the result of fertilization as GOTTSCHE ('58) believed. The archegonium shown in *fig. 33* was found in the involucre shown in *fig. 28*. Since the archegonium is practically ripe it seems evident that the fertilization of most if not all of the archegonia must take place before the mouth of the involucre is much contracted. The size of many involucres containing embryos points to

the same conclusion. It may still be, however, that the unusually long neck of the archegonium is of advantage in insuring fertilization, as suggested by LEITGEB ('77, p. 65) and RUGE ('93), though the involucre is not so nearly closed at the time of fertilization as they apparently supposed.

The wall of the venter of the archegonium becomes two-layered before fertilization. After fertilization, as the embryo develops, the venter increases greatly in length and in thickness, forming thus a long tubular calyptra which may be twelve or fifteen cells thick near the base (*figs. 31, 39, 41*). This calyptra is ultimately ruptured near the top by the elongation of the seta, in such a manner usually as to leave it more or less two-lipped.

### THE SPOROGONIUM.

The actual fertilization of the egg was not observed. At some time after the maturation of the archegonium, the neck shrivels at the tip, the wall of the venter begins to thicken; the egg then increases in size and cell divisions appear in it (*fig. 38*).

Material was not available for the determination of the sequence of the earliest divisions of the embryo, and from the youngest ones seen it could not be discovered whether these were longitudinal or transverse. That longitudinal walls appear very early is evident from *fig. 36*, and the transverse wall near the middle in this figure may be the primary one of the embryo, as is usual with other liverworts. That there is a quadrant formation in the upper part of the embryo is evident from *figs. 41, 42*.

The differentiation of foot and capsule appears early in the development and is indicated by the more rapid enlargement in diameter of the former and by the larger cells of which it is composed (*figs. 31, 38, 39, 40*). The capsule later increases in diameter so as slightly to exceed the foot, and becomes elongated to eight or ten times its diameter (*fig. 31*). The seta is developed from just above the constricted region that first marks the separation of foot and capsule (*figs. 31, 38, 40*). Later on this constriction is obliterated, the foot and seta differ little in diameter (*fig. 31*), and the foot is not as sharply distinguished from the rest of the sporogonium as is shown by GOTT-SCHE ('59, *fig. 17*).

The longitudinal walls which immediately follow the quadrant-walls in the capsule do not appear in very regular order, but there is soon discoverable an inner series of six or eight cells surrounded by an outer layer of about twice as many cells (*figs. 37, 41, 42*). The latter series form the wall of the capsule, while the former give rise to the spores and elaters (*figs. 40, 43, 44, 45*). Apparently no further periclines are formed in these primary wall cells, except at the top of the capsule (*figs. 31, 45, 48*). Thus all but this portion of the wall is a single layer of cells as described by GOTTSCHE ('58). I have seen no authority for the statement by SCHIFFNER ('93) that the wall is two-layered.

These cells of the wall of the capsule, as has been carefully described by GOTTSCHE ('58), have their walls provided with an elaborate series of thickening bands. The cells of the basal part of the wall are elongated to five to ten times their width, while those at the top of the capsule are nearly equal in length and in tangential width, though somewhat irregular in shape. The rupture of the ripe capsule originates at the top and extends down one side to allow the smooth-edged flaps to open out to the spoon-like form figured by HOOKER ('20). The mature capsule is about $1.5^{mm}$ in diameter and $6–8^{mm}$ long.

The seta of the nearly ripe capsule is about $1^{mm}$ long and in the final stretching to elevate the capsule increases to $30–40^{mm}$. Before stretching, the sporogonium has a nearly horizontal position in the involucre, but as the seta extends it curves upward and the capsule finally becomes vertical in position.

Just before elongation the component cells of the seta are $30–35\mu$ wide and $12–16\mu$ long. During elongation the width of the cells changes but little, while the length increases often to $0.5^{mm}$.

The division of the archesporial cells in the interior of the capsule goes on without evident differentiation until there are about 30 or 40 cells on a diameter of the capsule (*figs. 43, 44*). Soon after this the cells elongate markedly in a direction longitudinal to the capsule (*fig. 45*.) When their length has reached five to ten times their diameter (*fig. 46*), some of the thicker cells divide transversely and each gives rise to eight cubical spore mother-cells. Other more slender cells continue to elongate greatly to form the elaters (*fig. 47*). The elater-

forming cells are thus not sister cells of the spore mother-cells, but rather of cells which give rise to several of the latter. The longitudinal grouping of the spore mother-cells in *figs. 47* and *49* indicates their origin, and the pointed, terminal mother-cell of each row in *fig. 47* recalls the spindle-like form of the parent cell.

When the capsule is about three quarters grown, that is when it is 3 or 4$^{mm}$ long, the spore mother-cells round off from one another. Soon afterward they assume the usual four-lobed form (*fig.49*). Then follows the division of the nucleus and the separation of the spores of the tetrad in the usual manner. The mature spores are uninucleate, nearly globular, 16 to 18$\mu$ in diameter, and have a thick, reticulated wall (*figs. 51, 52*).

The elaters continue to elongate as the spores are maturing and ultimately reach a length of 150$\mu$. They are about 8$\mu$ in diameter in the middle, and taper to a rather blunt end in each direction. Some time after the individual spores are formed two rather closely twisted, spiral, thickening bands appear in each of the elaters (*fig. 50*). These bands are about as wide as the interspaces of thinner wall left between them. One of the bands often disappears considerably before the other as the end of the elater is approached. No grouping of the elaters or attachment to the wall of the capsule was noticed, except the attachment of a few scattered elaters at the base of the capsule to the wall near the end of the seta.

The elongation of the seta occurs after the capsule is practically ripe, and the latter opens soon after being pushed out of the involucre. The opening seems to proceed gradually, and the escape of the spores, aided by the twisting and untwisting of the elaters, is thus distributed over a considerable portion of time.

### CONCLUSIONS.

HOOKER ('20), GOTTSCHE ('58), and LEITGEB ('77, p. 62, and '81, p. 132) all recognized the similarity of Monoclea in size and habit to the Marchantiaceae, and LEITGEB noticed the likeness in the structure of the antheridium and the male receptacle to those of the same group of liverworts. But the form of the involucre, the structure of the archegonium, and especially the absence of air chambers and (as they believed) of tuberculate rhizoids, led all these workers to keep Monoclea out of the Marchantiaceae.

GOEBEL ('98, p. 240) points out the similarity in the development of the antheridium of Monoclea to that of the Marchantiaceae, which was figured (but apparently not recognized) by RUGE ('93), but still GOEBEL does not definitely include Monoclea in that family.

CAMPBELL ('98) for the first time placed Monoclea definitely in the Marchantiaceae, because of the form of the thallus and the presence of two types of rhizoids, but especially because of the structure of the male receptacle and of the antheridium and archegonium.

Practically all the evidence collected in the present research seems to the writer to favor the view of CAMPBELL. For it is found that the thallus of Monoclea is like that of the Marchantiaceae in gross structure, in the mode of growth and branching, in the type of initial cell, and as I have been able to show in the possession of tuberculate rhizoids as well as thin-walled ones, in which latter character Monoclea differs from all described Jungermanniaceae.

These tuberculate rhizoids have been overlooked by earlier observers probably because of their comparative rarity, and because of the very few tubercles present in each rhizoid (*figs. 23, 24*). The tuberculate rhizoids are 10 to 15$\mu$ in diameter, while the other rhizoids are 25 to 35$\mu$ in diameter and much thinner walled. The distribution of these two types of rhizoids is perfectly constant, as was shown by LEITGEB ('77, p. 63). The thick-walled ones are scattered more generally over the thallus, and always lie nearly parallel to it, while the thin-walled ones are clearly grouped near the mid-line of the thallus and stand out perpendicularly to it (*figs. 8, 9, 28*). This is just the relative position of these two types of rhizoids in, for example, Marchantia or Fegatella (CAVERS '04, *fig. 17*), where the tuberculate rhizoids arise under the ventral scales along the whole costa and run backward between these scales to the base of the thallus, while the large, thin-walled ones arise in groups and stand straight out from the thallus.

The tuberculate rhizoids of Monoclea are always thin-walled near the distal end, which probably means that there is a long-continued growth in length in this region. Some of them surely reach a very great length.

The absence of the ventral scales characteristic of the other Marchantiaceae, and of the air chambers with their chlorophyll-bearing cells, is probably, as CAMPBELL has suggested, to be regarded

as a reduction due to the nature of the habitat of Monoclea. For, though these plants are not actually submerged, they do live in very wet places and are surrounded by a constantly saturated atmosphere. COKER ('03) has shown that we have an actual example of this sort of reduction in *Dumortiera hirsuta*, plants of which growing in a damp atmosphere on a porous, sandy soil, had well-developed air chambers, while other plants which were constantly wet with dripping water had no trace of such chambers. Even in Marchantia I find that, as was shown by RUGE ('93), submerged plants have imperfect air chambers or none at all. There seems also to be a marked reduction in the size of the ventral scales, in the number of tuberculate rhizoids, and likewise in the number of tubercles in them in these submerged plants.

The facts of vegetative structure referred to strongly indicate a relationship with the Marchantiaceae, and the structure and development of the reproductive organs seem to me to confirm this beyond reasonable doubt.

The male receptacle of Monoclea does not, it is true, closely resemble that of Fegatella, with which it has been most frequently compared, since it has but one growing point, while that of Fegatella has several, as has been shown by LEITGEB ('81, p. 95) and CAVERS ('04). In this respect Monoclea resembles much more certain other genera of the Marchantiaceae. In Corsinia, for example, according to BISCHOFF ('35, pl. 70) and LEITGEB ('79, p. 48), the antheridia arise acropetally on an elongated, thickened, and bordered receptacle very like that of Monoclea in origin and structure. Similar also are the less known male receptacles of Funicularia, according to MONTAGNE ('56), and of Sauteria, according to BISCHOFF ('35) and LEITGEB ('81). Among the higher Marchantiaceae also male receptacles similar to that of Monoclea are not wanting. Thus Aytonia (LEITGF '81, GOEBEL '98), Reboulia (BISCHOFF '35, LEITGEB '81), Grim (BISCHOFF '35, LEITGEB '81), and especially Fimbriaria (B '35, CAMPBELL '95) show a striking resemblance to Monoc usually structure and development of the male receptacle. O g like that of hand there is no structure closely comparable with th tacle of Monoclea known among the Jungermanniac formed in acro-

The development and structure of the sunken an bles rather that ilar

clea is still more clearly marchantiaceous in type. The large number of primary transverse divisions in the young antheridium, the mode of separation of the primary spermatogenous cells from the wall cells, and the elongated pointed form of the mature antheridium are, I believe, not found in any of the Jungermanniaceae.

The development of the archegonia directly upon the dorsiventral vegetative part of the thallus has, as was noted above, always been considered a most important difference between Monoclea and the Marchantiaceae, most workers having on this account compared it rather with the genera Pellia and Symphyogyna of the Jungermanniaceae. But even in this feature Monoclea is not without counterparts among the Marchantiaceae. For example, in Funicularia, according to LEITGEB ('79, p. 59) the archegonia are formed in groups of three or four, each group being sunken in a pit in the dorsal side of the thallus and protected by a hood-like involucre, which grows out over the archegonia from behind. Likewise in Corsinia, according to the same author ('79, p. 55), the archegonia arise acropetally in groups of eight or ten exactly as in Monoclea, and are also covered by a similar hood, which however seems to develop after fertilization. This hood may cover all the fertilized archegonia in one pit or there may be several hoods in the same pit, each covering one or more archegonia. In both genera of the Targionioideae (Targionia and Cyathodium) the archegonia arise directly behind the growing point of an ordinary branch of the thallus (LEITGEB '81, pp. 133 and 139, and CAMPBELL '95, p. 54). The two-lobed outgrowth of the thallus found here resembles in origin the involucre of Monoclea, though it remains quite small until after fertilization.

It seems more probable that in the case of Corsinia the wall of the pit as a whole is homologous with the involucre of Monoclea, rather than that each of the hoods is, but the most important character which bet____oclea has in common with Corsinia, as well as with the other walle____ mentioned, is the development of the archegonia on an

The t____ ized portion of the thallus.
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great length. ____ g neck and especially in the six rows of neck cells it
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bearing cells, is prob

Probably the most serious obstacle of all to putting Monoclea in
the Marchantiaceae has been the sporogonium, which with its long
seta and its erect cylindrical capsule has quite the aspect of that of
certain of the frondose Jungermanniaceae. But even here distinctive
marchantiaceous characters are not entirely wanting. Thus, for
example, the wall of the capsule of Monoclea is a single layer of cells
(*figs. 31, 43*), except near the base and a small area at the top. In this
respect it agrees with all known Marchantiaceae (SCHIFFNER '93),
and differs from all the Jungermanniaceae with which it has been
supposed to be related. For the wall of the capsule of Pellia is well
known to be three or four-layered, and I have found that of Sym-
phyogyna to have a similar structure, instead of a one-layered wall
as is stated by SCHIFFNER. The slightly developed foot of Monoclea
has many counterparts among both Marchantiaceae and Junger-
manniaceae. The seta is probably longer than is found in any other
marchantiaceous form, but this and the simple type of rupture of the
capsule, which occurs in isolated cases in both the Jungermanniaceae
and Anthocerotaceae, are perhaps related in some way to the peculiar
habitat of the plant. The spores and elaters show, so far as I have
discovered, no characteristic peculiarities.

The particular genus of the Marchantiaceae to which Monoclea
is most closely related I am at present unable to suggest. We have
seen that it resembles certain of the simpler genera in the place of
origin of its antheridia and archegonia. These facts seem to me to
favor CAMPBELL's view ('98) that the relationship of Monoclea is with
the lower Marchantiaceae. The occurrence of similar male recep-
tacles in some of the higher forms, *e. g.*, Fimbriaria and Grimaldia,
is probably an instance of the persistence of the primitive type of male
receptacle side by side with a more highly specialized female one.

### SUMMARY.

Monoclea occurs in Jamaica in very damp places, being usually
constantly wet with dripping water.

The male receptacle of Monoclea is only superficially like that of
Fegatella, since all the antheridia of a receptacle are formed in acro-
petal succession from one growing point. It resembles rather that
of Corsinia and Fimbriaria.

The antheridium rudiment is elongated, and it divides transversely into six or seven primary cells. The wall cells and spermatogenous cells are separated from each other in the body of the antheridium after the formation of quadrant and octant walls. The mature antheridium is elongated and pointed and is sunken in the receptacle.

In the nucleus of the spermatozoid the individual chromosomes are recognizable as distinct twisted fibers.

The archegonium is very long-necked, has six rows of neck cells and twelve or more neck canal cells. It is probably fertilized before the hood-like involucre has grown far beyond its tip.

The capsular portion of the sporogonium divides to quadrants and octants before sporogenous cells and wall cells are separated. The foot is small, the seta stretches to 30 or 40$^{mm}$ in length, and the extended capsule is erect, elongated, cylindrical, and its wall is a single layer of cells.

Monoclea possesses two kinds of rhizoids, corresponding to those of Marchantia in size, direction of growth, and in the presence of tubercles in those of one type.

The absence of air chambers and ventral scales is probably due to the nearly aquatic habit of the plant.

The evidence gained from the study of the origin and structure of the male receptacle, and of the antheridium and archegonium, and from the structure of the wall of the capsule, and the presence and direction of growth of the two types of rhizoids, favors the view that Monoclea is most closely related to the lower Marchantiaceae.

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## EXPLANATION OF PLATES XVI AND XVII.

### PLATE XVI.

FIG. 1. View of upper surface of part of a male thallus, showing branching and three generations of male receptacles. ×1.5.

FIG. 2. Transverse section of a male plant through a mature receptacle. ×5.

FIG. 3. Longitudinal section of male plant through receptacles of two generations. ×3.

FIG. 4. Diagrammatic view of upper surface of a half-grown male receptacle with a single growing point; the dotted outlines indicate the location of the antheridia. × 25.

FIG. 5. Similar view of a male receptacle with two growing points. × 25.

FIG. 6. Upper anterior part of a longitudinal section of a young male receptacle, showing very young antheridia. × 350.

FIG. 7. Longitudinal section of a young male receptacle, passing just at one side of the growing point; the dotted lines indicate the position of the growing point in an adjoining section. × 38.

FIG. 8a. Surface view of nearly mature spermatozoid, showing the intertwisted chromatin fibers. × 1500.

FIG. 8b. Diagram of an optical section of such a spermatozoid, showing the relation of chromatin fibers still more clearly. × 4000.

FIG. 9. Median longitudinal section of an older male receptacle; the letters indicate the order of origin of the antheridia. × 30.

FIG. 10. Young antheridium and surrounding cells from a section similar to last. × 350.

FIG. 11. Longitudinal section of a young antheridium, showing the seven primary tiers of cells and the separation of the wall cells from the spermatogenous cells. × 350.

FIG. 12. Similar section of a slightly older antheridium. × 350.

FIG. 13. Similar section of an antheridium and an antheridial cavity of the male receptacle. × 350.

FIG. 14. Longitudinal section of an older antheridium. × 160.

FIG. 15. Transverse section of a young antheridium and surrounding cells showing a primary longitudinal wall of the antheridium. × 650.

FIG. 16. Similar section of an antheridium showing quadrant walls. × 650.

FIG. 17. Similar section of an antheridium in which spermatogenous cells and the antheridial wall have been differentiated. × 650.

FIG. 18. Transverse section of an older antheridium, showing the mode of division of the four primary spermatogenous cells. × 350.

FIGS. 19–20. Similar sections of still older antheridia, showing multiplication of spermatogenous cells. × 160.

FIG. 21. Portion of longitudinal section of nearly mature antheridium, showing the wall and the three-cornered spermatozoid mother-cells. × 350.

FIG. 22. View of the upper surface of part of a female plant, showing an involucre containing two young sporogonia, one containing a nearly full-grown sporogonium, and one from which a capsule has already been extended. × 1.5.

FIGS. 23–24. Optical longitudinal sections of tuberculate rhizoids. × 650.

FIG. 25. Portion of the edge of the thallus with thick-walled marginal rhizoids. × 160.

FIG. 26. Longitudinal section through the growing point of a female plant, showing the beginning of the pit in which the archegonia arise. × 75.

*PLATE XVII.*

FIG. 27. Lower portion of the same section, showing the slime-secreting hairs and the cells which are to form archegonia. × 350.

FIG. 28. Longitudinal section of an older archegonial pit, showing the half-grown involucre and two mature archegonia. × 38.

FIG. 29. Similar section of a full-grown involucre, containing an archegonium with a young embryo. × 8.

FIG. 30. Transverse section of fertile branch of female thallus passing through an involucre containing a nearly mature sporogonium. × 8.

FIG. 31. Longitudinal section of similar involucre and sporogonium. × 8.
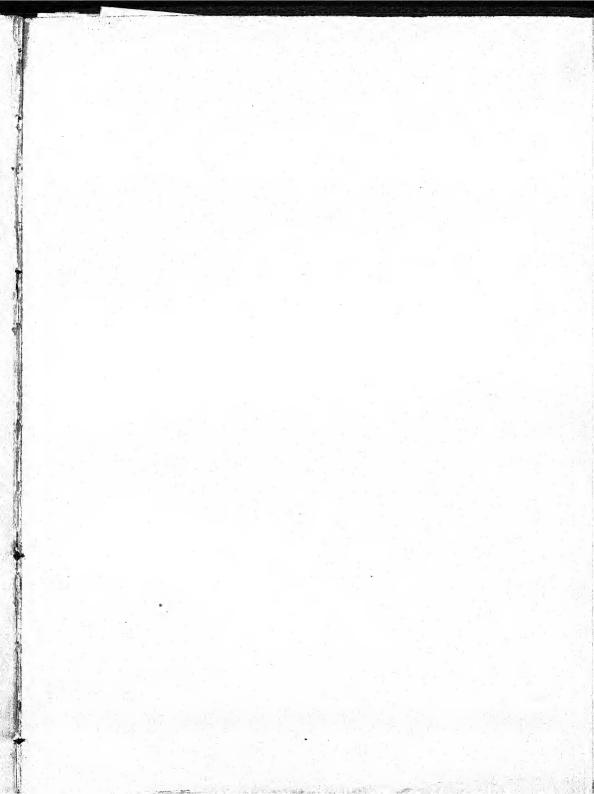
FIG. 32. Longitudinal section of a young archegonium. × 350.
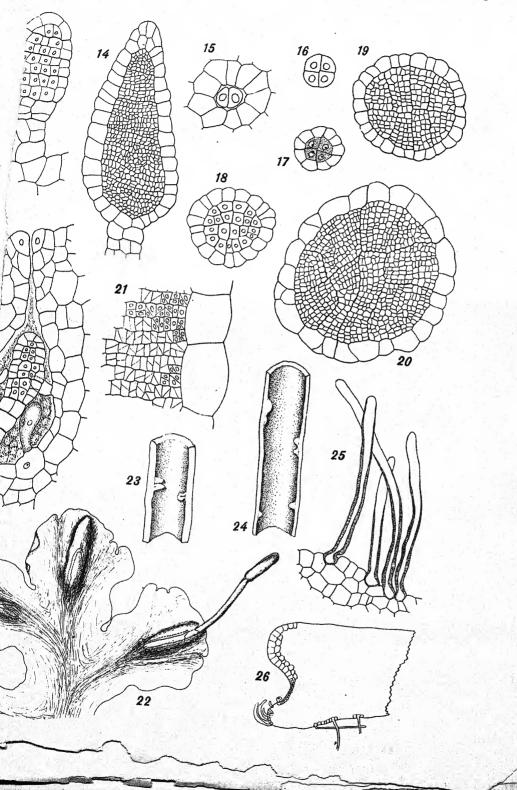
FIG. 33. Longitudinal section of a mature archegonium. × 160.
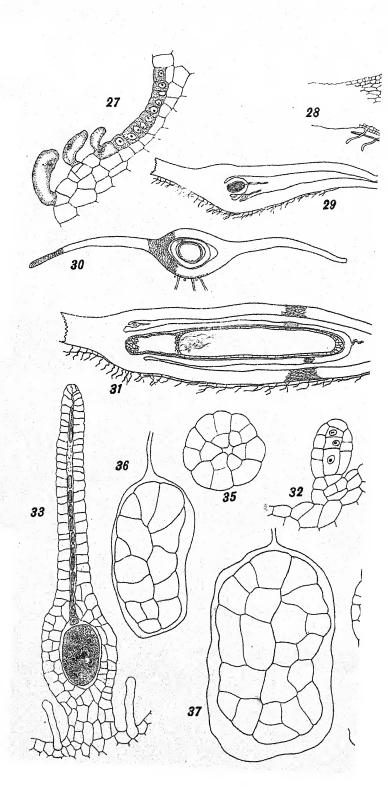
FIG. 34. Transverse section of neck of archegonium, showing eight neck cells. × 160.
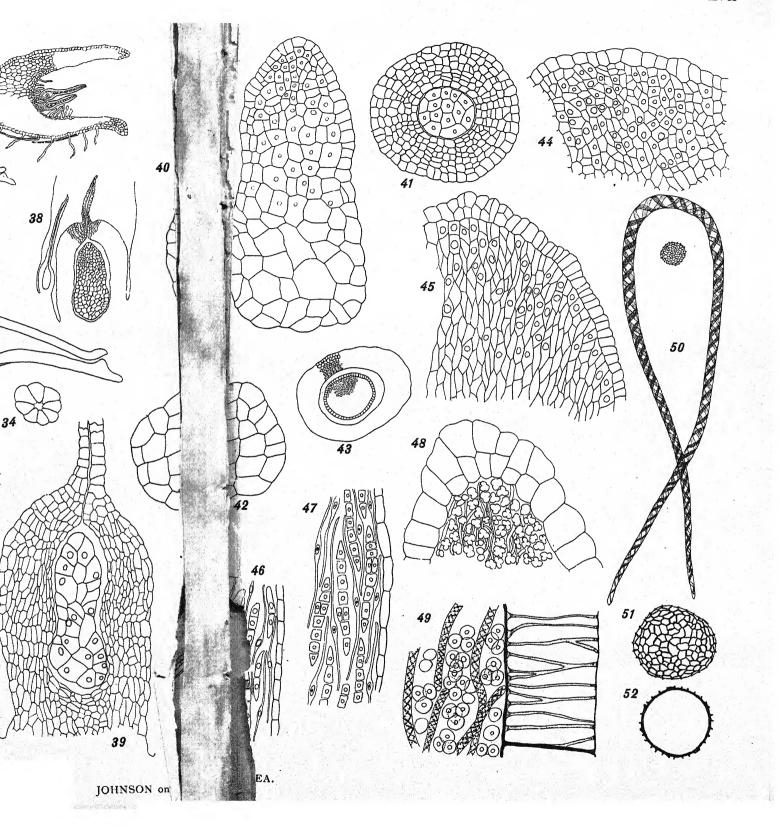
FIG. 35. Similar section of archegonium at juncture of neck and venter, showing a normal six-celled neck. × 300.

FIGS. 36–37. Longitudinal sections of young embryos, showing the earlier walls in the latter. × 350.

PLATE XVI

PLATE XVII

*38*

*40*

*34*

*39*

*41*

*44*

*45*

*42*

*43*

*48*

*47*

*46*

*49*

*50*

*51*

*52*
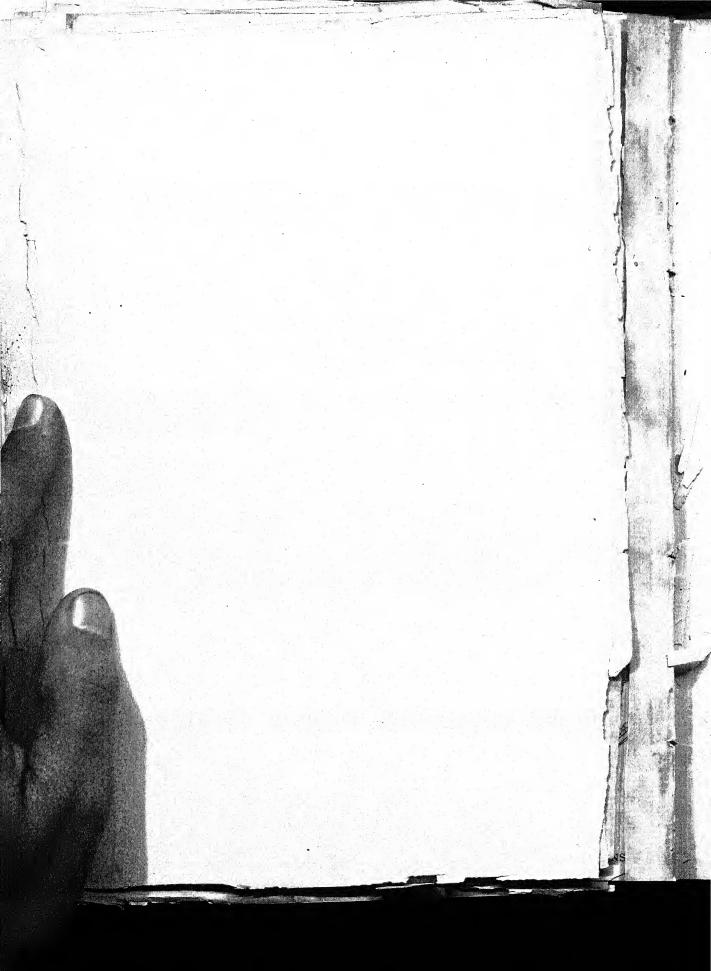
FIG. 38.  Longitudinal section of young embryo and archegonium.  ×38.

FIG. 39.  Similar section with a slightly younger embryo, showing the differentiation of the latter into foot, seta, and capsule.  ×160.

FIG. 40.  Longitudinal section of an older embryo, showing differentiation of capsule into wall and sporogenous cells.  ×160.

FIG. 41.  Transverse section of an archegonium and embryo of the age of that shown in *fig. 37*, showing arrangement of cells in the capsular region.  ×160.

FIG. 42.  Similar section of another embryo.  ×160.

FIG. 43.  Transverse section of an archegonium, with an embryo showing wall of capsule and isodiametric sporogenous cells.  ×38.

FIG. 44.  Detail of last.  ×350.

FIG. 45.  Part of longitudinal section of a capsule of the same age as the last.  ×350.

FIG. 46.  Part of a similar section of an older capsule, showing elaters and their spindle-shaped sister cells dividing to spore mother-cells.  ×350.

FIG. 47.  Similar figure from an older capsule, showing elaters and rows of spore mother-cells.  ×350.

FIG. 48.  Longitudinal section of the tip of a nearly mature capsule, showing two-layered region of the wall and three-lobed spore mother-cells.  ×160.

FIG. 49.  Elaters, tetrads of spores and a cell, from the wall of a still more mature capsule.  ×350.

FIG. 50.  Single elater from a ripe capsule.  ×700.

FIG. 51.  A single spore showing structure of spore wall.  ×1250.

FIG. 52.  Optical section of spore wall.  ×1250.

# ON THE SPORES OF CERTAIN CONIFERAE.

W. C. COKER.

(WITH TWENTY-FOUR FIGURES)

THE POLLEN GRAIN.—There is much greater diversity in the male gametophyte of gymnosperms than of angiosperms. Such forms as Thuja, Taxodium, and Taxus have this structure so much reduced as closely to resemble, in the number of cells formed, the pollen grains of the flowering plants. Others, as Ginkgo, Pinus, and Podocarpus, contain, sooner or later, as many as six nuclei in the pollen grain and tube. In my paper on Taxodium I have summarized the present knowledge on this point in gymnosperms, and it is seen that much yet remains to be done before the structure of the pollen tube is understood in all genera.

During the spring of 1902, while in Bonn, I examined almost daily the maturing pollen grains of a number of conifers, and followed them to the time of shedding. This was for the purpose of settling the point as to whether it were possible that a sterile prothallial cell or cells might be cut off early in development and, becoming disorganized, be overlooked in the ripe grain.

In the following species it was found that no division whatever occurred in the pollen grains while they were in the sporangium, and that they were shed in the one-celled stage: *Cupressus Goveniana, C. macrocarpa, C. Benthamiana, Taxus baccata* and vars. *epacrioides, fastigiata, cuspidata,* and *adpressa, Juniperus sphaerica, J. chinensis.*

In *Cupressus sempervirens,* pollen from a tree growing in the warm-house showed a division while still in the sporangium; but this variation from the rule in this genus probably resulted from delay in the dehiscence of the sporangium, caused by the unnatural conditions. It could easily be seen that dehiscence did not occur promptly and in some cases was only partial. Pollen grains of *C. Benthamiana* placed in sugar solution divided in a few cases in about a week.

In the following species there was one division of the pollen just

[September

before shedding: *Chamaecyparis Lawsoniana pendula, C. sphaeroidea, C. chinensis, C. obtusa, C. pisifera, Callitris* sp., *Cryptomeria japonica* and var., *Thuja orientalis.*

The fate of these pollen cells was not followed further, but the appearance of the small cell cut off before shedding is quite unlike that of a prothallial cell, and bears every resemblance to the single (generative) cell cut off at the same time in Taxodium, where certainly no prothallial cell is formed. Furthermore, in · all cases where prothallial cells are known to occur, they are produced while still in the sporangium, and the divisions that cut them off are immediately followed by another which gives rise to the generative cell. It is hardly to be doubted, therefore, that no prothallial cell is formed at any time in the species above mentioned.
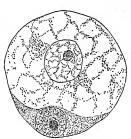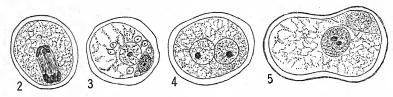
FIG. 1. *Thuja orientalis;* pollen grain ready to shed. × 1700.

In *fig. 1* is shown the mature pollen grain of *Thuja orientalis,* the exine not being drawn. The generative cell is of the usual structure and is sharply separated from the rest of the contents. Its nucleus is as usual more dense than the tube nucleus. In *fig. 2* the pollen grain of *Cupressus sempervirens* is represented in division, while in *fig. 3* the division is completed. In this last figure a few starch grains are shown. In most cases the generative cell is free from starch even

FIGS. 2–5. *Cupressus sempervirens; fig. 2,* pollen grain in division; *fig. 3,* same ready for shedding; *figs. 4* and *5,* abnormal pollen grains. × 750.
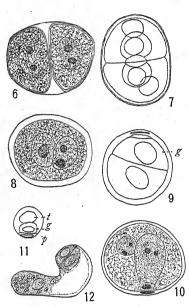
in pollen where it is abundant, but here (*fig. 3*) it also contains a few scattered grains.

It will be seen that the above results confirm to a large extent STRASBURGER'S observations on mature pollen. He finds[1] that in

[1] Ueber das Verhalten des Pollens, etc. 1892.

species of Taxus, Cupressus, and Juniperus the pollen grain divides only after reaching the nucellus; while in Thuja, Cephalotaxus, Podocarpus, Chamaecyparis Lawsoniana, Cryptomeria, Sequoia, Araucaria, and the Abietineae it divides before shedding.

In examining so many pollen cells it was not surprising that a good many abnormal forms were met with. In Cupressus it happened not infrequently that the generative nucleus was not cut off in a separate cell of its own, but remained free in the general cytoplasm, side by side with the pollen tube nucleus. In such cases (*fig. 4*) the two nuclei were so much alike as to be hardly distinguishable. In *fig. 5* is illustrated a pollen grain of peculiar shape and about twice the normal size. The generative cell, however, is of the usual appearance. It will be remembered that the tree from which this pollen was taken was not growing in perfectly congenial surroundings, and this may account for the rather unusual number of abnormalities.

FIGS. 6–10. *Larix europaea; figs. 6–9*, abnormal pollen grains; *fig. 10*, normal grain. × 315. FIGS. 11, 12. *Encephalartos* sp.; *fig. 11*, shed pollen grain; *fig. 12*, sprouting grain. ×315.
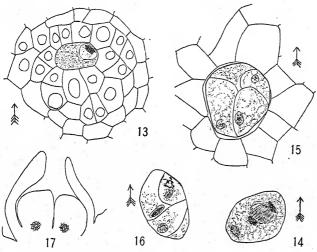
In *Larix europaea* a number of cases were found in which the mother-cells had divided but once, so that only two instead of four pollen grains were formed (*fig. 6*). In some of these double grains the divisions proceeded about as usual. *Fig. 7* gives such a case, but here only one prothallial cell is evident. Abnormal grains with two large free nuclei were also found (*fig. 8*). In *fig. 9* a generative cell (*g*) of very unusual appearance is shown. For the sake of comparison a drawing is given of the normal pollen grain of Larix (*fig. 10*).

In *Encephalartos* sp. ? the mature pollen grain contained one prothallial cell, *p*, a generative cell, *g*, and a tube cell, *t* (*fig. 11*). No

starch was found at this stage, but when the pollen was put in sugar solution it made its appearance in about two days. A sprouting grain that had been in sugar solution six days is shown in *fig. 12*. Here the prothallial cell and the generative cell are changed in position and the tube nucleus has moved down, and is surrounded by starch. One prothallial cell has been found in Ceratozamia, Zamia, and Cycas.[2]

THE MEGASPORE AND EMBRYO SAC.—In the Cupressineae there is practically nothing known of the behavior of the megaspore mother-



FIGS. 13–17. *Thuja orientalis; fig. 13*, megaspore mother-cell surrounded by spongy tissue, × 335; *fig. 14*, megaspore mother-cell during first division, × 525; *fig. 15*, tetrad of megaspores, × 525; *fig. 16*, the same, × 525; *fig. 14*, abnormal ovule with two sporongia, × 43.

cell or of the origin of the megaspore. In Taxodium, which I consider as belonging to this group, the megaspore mother-cell divides into three potential spores, the largest of which is functional. As to other members of the group there is scarcely any literature that treats of this stage. STRASBURGER[3] remarks that in Thuja the origin of the embryo sac is essentially as in Taxus.

[2] The literature on this point is cited in my paper on Taxodium.

[3] Die Angiospermen und die Gymnospermen. 1879.
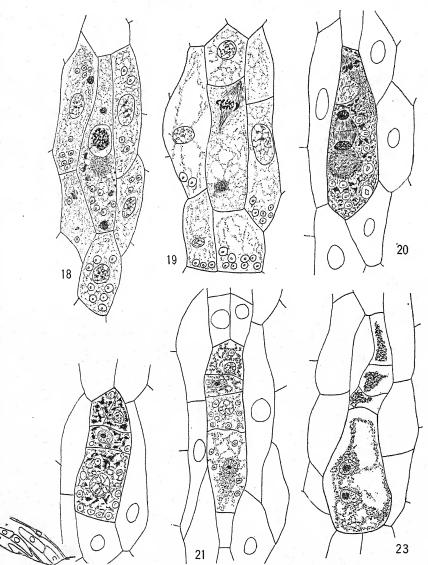
*Thuja.*—In the hope of settling these points in some member of the Cupressineae, young ovules of *Thuja orientalis* were collected and sectioned in Bonn. The megaspore mother-cell soon becomes evident among the conspicuous spongy tissue. It has thicker walls and is also less dense than the cells around it. Its position is not always in the center of the spongy tissue, and its long diameter is as often as otherwise at right angles to the longitudinal axis of the ovule (*fig. 13;* the arrow shows the direction of the axis of the ovule). Occasionally there are two or three mother-cells developed, and in such cases they are generally separated by cells of the spongy tissue. In *fig. 13* the mother-cell nucleus is in synapsis, and in *fig. 14* the first division spindle is shown. There is the same kinoplasmic mass at the lower end of the cell as in *Larix sibirica*[4] and Taxodium. The spindle of the next division was not seen, but the result is shown in *figs. 15* and *16.* Four megaspores are produced and their arrangement is more nearly that of the typical tetrad than in any other gymnosperm in which this stage has been described. After the completion of the last division, the spores may be seen packed together within the still nearly round mother-cell. They are never in a straight row, but are so arranged that in thin sections no more than three nuclei appear at once. The mother-cell wall around them also stains more deeply than those of the neighboring cells, so that the appearance approaches very closely what is found in the divided mother-cell of ferns. None of the spores is conspicuously larger than the others, and it was not determined which one became functional.

A peculiar abnormality in the ovule of *Thuja orientalis* is given in *fig. 17.* Two separate nucelli are present within the same sporangium and each has the usual sporogenous area. In other cases two fused sporangia were found in the same ovule, the sporogenous areas still being distinct. I have a preparation showing the same peculiarity in the ovule of *Erythronium americanum;* the nucellus is two-lobed and contains an embryo sac in each lobe.

*Taxus.*—Strasburger finds[5] several megaspore mother-cells developed, and says that one or more of them divide into three or rarely

4 JUEL, H. O., Beiträge zur Kenntniss der Tetradentheilung. Jahrb. Wiss. Bot. 35:626–659. *pls. 15–16.* 1900.

5 Die Angiospermen und die Gymnospermen. 1879.

FIGS. 18–23. *Taxus baccata;* *fig. 18,* megaspore just before division, nucleus in synapsis, × 675; *fig. 19,* same during first division, × 675; *fig. 20,* spindles of second division, × 675; *fig. 21,* four potential megaspores in a row, × 525; *fig. 22,* four potential megaspores, the upper lying side by side, × 525; *fig. 23,* sprouting of lower megaspore, × 625.

more cells lying in a row. JÄGER[6] with some hesitation agrees with STRASBURGER that there are three or four megaspores formed from the mother-cell; but it is pretty evident from his figures that he had before him not the spores, but the mother-cells and sterile tissue. JÄGER also seems to agree with STRASBURGER that there may be sev-
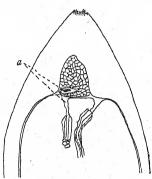
FIG. 24. *Taxus canadensis;* two prothallia in same ovule; embryos in lower, disorganizing archegonium in upper. × 43.

eral megaspore mother-cells. I cannot confirm these two observers as to the number either of the megaspore mother-cells or of the potential megaspores into which they divide. In my preparations there is no evidence that there is ever more than one megaspore mother-cell formed. The mother-cell is here harder to distinguish than in any other plant I have seen. At the time its first division occurs, it is long and narrow, resembling closely in shape the cells adjoining (*figs. 18* and *19*). It differs from them, however, in the possession of a rather conspicuous kinoplasmic mass near its lower end, resembling in this respect the mother-cells in Larix, Taxodium, and Thuja. Very rarely there is another smaller kinoplasmic mass above the nucleus. In *fig. 18* the mother-cell is shown in the center with its nucleus in synapsis. The first division is given in *fig. 19*. The spindle as here shown is at the upper end of the cell, and the division results in cutting off a small upper and a large lower part. The second division occurs simultaneously in both of these daughter-cells, as is shown in *fig. 20*. This results in the formation of four potential megaspores, which lie as a rule in a single row (*fig. 21*). The second division in the upper daughter-cell of the first division, however, may in some cases be at right angles to the longitudinal axis of the ovule, so that the two upper megaspores lie side by side (*fig. 22*). The long, narrow cells adjoining the megaspore mother-cell, which as mentioned above are well filled with starch, have remained undivided during these divisions. In some cases they divide into two, but they never resemble

[6] Beiträge zur Kenntniss der Endospermbildung und zur Embryologie von *Taxus baccata*. Flora **86**:241–288. *pls. 15–19.* 1899.

the megaspore mother-cells, nor do their divisions give rise to cells resembling the megaspores. There seems no doubt that Stras-burger and Jäger were wrong in giving the number of megaspores as generally three.

In addition to *Taxus baccata* and *Thuja orientalis* (as here shown) there are but three other conifers in which four potential mega-spores have been definitely described. They are *Larix sibirica*, *Pinus Laricio*, and *Sequoia sempervirens*.[7]

As mentioned above, there is no spongy tissue surrounding the megaspore mother-cell in Taxus, and as the lower megaspore develops in sprouting, it crushes aside and destroys the cells immediately adjoining it, eating its way gradually into the more distant layers (*fig. 23*).

Hofmeister observed many years ago that more than one embryo-sac may occur in Taxus, and this I have found to be not uncommon in *Taxus canadensis*. Here one of the two prothallia, when two are present, is usually much smaller than the other. It is interesting to find that both prothallia may bear archegonia (*fig. 24, a*). The archegonia in the upper prothallium face towards the lower prothallium and not toward the micropyle, showing that the upper prothallium is inverted. The pollen tube does not stop at the upper end of the nearest prothallium, but growing past it presses in between the two to reach the archegonia. In all such cases it was the archegonia of the lower prothallium only that were fertilized (*fig. 24*).

In conclusion I wish to thank Professor Strasburger for his valuable advice and unfailing kindness.[8]

[7] See my paper on Taxodium for literature.

[8] The drawings have been inked in by Mr. H. A. Allard under my direction.

# BRIEFER ARTICLES.

## ARTIFICIAL PARASITISM: A PRELIMINARY NOTICE.

SOME years ago, in the course of an investigation suggested by PFEFFER to show that ordinary roots, as well as those of parasites, can penetrate living tissues, I succeeded in growing a pea (*Pisum sativum*) on a plant of horse-bean (*Vicia Faba*), at least so far that the pea blossomed and set seed.[1] At intervals since that time I have grown peas on plants of the same bean, with success varying according to the very unideal conditions under which I have experimented. Some of the results obtained seem worthy of publication now, although I have only begun a piece of work which I hope to carry on for years to come.

The main object of the investigation is to ascertain how an independent plant will behave when compelled to lead a parasitic or partially parasitic existence; what the changes, immediate, successive, and cumulative, may be in successive generations.

The method so far pursued is this. Pea seeds of "extra early" varieties, soaked in water for twenty-four hours, are placed, radicle downward, in bulb pots of fine sand, and allowed to germinate until the radicles are $1-2^{cm}$ long. The seeds are now ready for setting on the beans. These are plants of *Vicia Faba*, $30^{cm}$ or more tall, grown two or three in each pot. Care is taken to select for experiment only strong plants, although I cannot see that the peas injure the beans on which they grow. At a height of about $15^{cm}$ above the soil I cut a hole, with a taper-pointed, sharp, clean scalpel, in the stem of the bean, the hole being about as large as the radicle of the pea selected for mounting on the bean plant. Into this hole the radicle is gently pushed, passing into the cavity of the hollow stem, until the cotyledons are close against the stem. A strip of writing paper is now so wrapped about the stem and fastened with sealing wax as to form a conical mold. Into this plaster of Paris is poured until it all but covers the cotyledons. In this way the pea is held in place without interfering with the upward growth of the plumule. In dry weather the molds are made deep enough to hold a layer of wet saw-dust $1^{cm}$ or more deep over the plaster. This is unnecessary, however, in damp weather. When the pea-plants are $5^{cm}$

[1] PEIRCE, G. J., Das Eindringen von Wurzeln in lebendige Gewebe. Bot. Zeit. **52**: 169–176. 1894.

or so high, I take off the paper and plaster, cut off the cotyledons, and thus force the peas to draw all their water and mineral salts from the bean plants. This they do successfully.

By such a simple method as this I compel peas to live on bean-plants in essentially the same degree of parasitic dependence as that of Viscum or Phoradendron upon oaks. What are the results? These will be shown by extracts from my laboratory notes.

January 27, 1902. Peas set November 12 on beans and in dirt in same boxes began to bloom; one flower on a bean-pea, several on soil-peas. Great difference in size of plants, number and area of leaves, size of flower and of parts of flower, between bean-peas and soil-peas. Weather since November 12 dry and cold for the most part.

These plants were grown out of doors in a cold frame on the southwest side of the laboratory building. The frame was usually open from nine or ten o'clock until four or five daily, the hours of opening and closing depending mainly upon the temperature. The boxes used were shallow and the soil poor. The soil-peas were about half the size which the plants of the same variety would attain later in the season in rich soil of proper depth. The bean-pea plants were about one quarter to one half the size of the soil-pea plants growing in the same boxes, but were well proportioned and stocky.

From these plants I harvested a crop of ten good seeds from the bean-peas and ninety-three from the soil-peas. On the bean-peas there were only two or three peas in a pod, and the pods were small and rather thin, splitting normally when dry.

These pea-seeds I subsequently measured by vernier caliper. The air-dry, ripe seeds were not uniform in shape, and rather than take the largest diameter in each case I decided to measure through the same points, as nearly as possible, in each seed, viz., on a line bisecting the hilum at a right angle, holding the hilum toward my lefth and, the caliper being in my right. Of the bean-peas three were decidedly smaller than the rest.

Thickness of smallest bean-pea seed.....................5.25$^{mm}$
Thickness of largest bean-pea seed......................6.95
Average thickness of 10 bean-pea seeds..................6.31
Average thickness of  7 larger bean-pea seeds...........6.66
Average thickness of  3 smaller bean-pea seeds..........5.48

I measured similarly the 93 seeds, ripe and air-dry, which I had gathered from the pea-plants grown in the soil. Three of these peas were more than 8.00$^{mm}$ in thickness, one was 5.12$^{mm}$. This last was smaller than any bean-pea. There were also fifteen among these soil-peas which were

less than 6.00$^{mm}$ in thickness. The average thickness of 93 soil-peas was
6.88$^{mm}$.

The weights, air-dry, of the bean-peas and soil-peas were

|  | Bean-peas | Soil-peas |
|---|---|---|
| Total weight | 1.709$^{gr}$ | 20.111$^{gr}$ |
| Mean weight | 0.170 | 0.216 |
| Largest weighed | 0.227 | 0.337 |
| Smallest weighed | 0.090 | 0.119 |

Comparing these sizes and weights of the seeds with the sizes of the
plants, we see that the individual seeds are much less reduced in size and
weight by the enforced semi-parasitism of the parents than are the vege-
tative parts.

I subsequently soaked these seeds, the ten and the ninety-three, in sepa-
rate dishes of tap-water, for twenty-four hours. The bean-peas then
weighed 3.363$^{gr}$, the soil-peas 32.449$^{gr}$. The bean-peas, therefore, gained
1.967 times their weight, the soil-peas 1.613 times. From this it may be
inferred that the bean-peas either were thinner skinned or contained more
actively absorbing substances than the soil-peas. Which was the case I
cannot tell.

The bean-peas were then placed (2:00 P.M., May 5, 1903) in wet sphag-
num to root. On May 6, 4:00 P.M., good normal roots 1$^{cm}$ long had been
formed by six of these seeds. I mounted them, as before described, on
potted plants of *Vicia Faba*. The following morning three more were set
on the bean plants. I broke the root of one of the ten seedlings in mounting
it, and therefore threw it aside. Thus I had, mounted on bean plants,
nine seedlings of peas grown the previous year on bean plants. These
seedling peas, therefore, had never been in contact with the soil. Never-
theless, in the tap-water and especially in the sphagnum there was a certain
amount of "dirt." This could be avoided, and will be in future experi-
ments.

During the succeeding weeks these peas grew into little plants, somewhat
smaller than those of the preceding season, but well proportioned and
healthy-looking. I moved them from the laboratory to my own garden,
where they would be watered during the summer vacation and where I
could watch them, but unfortunately a dog or some other creature played
havoc with my beans one day while I was away from home, and my experi-
ment was ended.

Something should be said, even in such a superficial account as this,
about the roots of the peas grown on beans, and of the relations of these
roots to the tissues of the beans. There was no tissue union between host

and parasite as in natural semiparasites like Viscum and Phoradendron. The roots grew downward through the internodes and nodes, but did not, in any case here reported, reach the level of the soil, much less reach the soil itself. The roots branched much less freely than normal soil roots, were closely applied to the walls of the hollow internodes, and did not at any point fill the cavity of the internode.

That this much reduced root-system sufficiently supplied the small bean-pea plants with water is proved by an accidental experience. The potted bean plants one day became dry enough to wilt, but the peas were perfectly fresh and turgescent. The beans recovered promptly when watered and the peas at no time showed any ill effects.

It may be claimed that the smaller size of the pea-plants grown on beans is due to hard times—to mechanical interference with the normal growth and development of the root system. This may be true, but it is equally true that there are mechanical hindrances to the growth, extension, and development of the root systems of all phanerogamic parasites. In this respect, therefore, the cases are parallel.

In the aerial parts of Viscum, Phoradendron, and Arceuthobium,[2] xerophytic characters are evident.[3] These did not appear in my bean-peas, unless the smaller number and size of the leaves and the shortened internodes may be so called. Xerophytic characters may appear later if peas are cultivated on beans through a series of generations. I hope to be able to do this, under conditions which can be carefully controlled, and especially where my plants may at least be protected against ordinary accident.

I have tried various other seeds on *Vicia Faba*, including *Vicia Faba* itself, but peas have so far done best and *Vicia Faba* has proved to be the best host for them. A more succulent plant with solid stem, however, would be better. This I shall try in the future.

Though this is an incomplete account of experiments far from concluded, it has seemed best to put this much of my work on record. It may throw a little light on questions regarding the beginning of parasitism, the immediate effects of removing the roots of green plants from their normal medium, the soil, and compelling these green plants to supply themselves with water and mineral matters from other plants.—GEORGE J. PEIRCE, *Stanford University, California.*

[2] I expect presently to publish a paper on Arceuthobium.

[3] CANNON, W. A., The anatomy of *Phoradendron villosum*. Bull. Torr. Bot. Club 28: 374–390. *pls. 27–28.* 1901.

## THE GROWTH OF RAMALINA RETICULATA.

### (WITH ONE FIGURE)

RAMALINA RETICULATA (Noehd.) Krempelh., so characteristic of the coast valleys of California, offers to the plant physiologist a particularly fruitful field for the study of the growth, apothecial development, and dissemination of lichens.

TUCKERMAN states[1] that his longest specimens were a little more than a foot in length, and that the widest perforated expansions exceeded 20$^{mm}$. Just what dimensions this plant may attain I am not prepared to state, but I agree with Dr. Peirce that it is probably the largest of our North American lichens. Specimens four and five feet long are common on the trees about Stanford University, their widest perforated expansions reaching two feet or more. Specimens in my herbarium vary from those of the most delicate lace-like structure to those having broad, unperforated expansions 25 to 40$^{mm}$ in width, dimensions much greater than the largest



FIG. 1.—*Ramalina reticulata:* A, thallus branch; B, lobe; C, knot of silk used to designate measured lobes.

perforated specimens seen by Tuckerman. *Usnea longissima* Ach. attains a length of eight or nine feet on the redwoods of the Santa Cruz mountains, but the thallus is so slender that its real size is much less than that of *Ramalina reticulata.*

The plant is evidently such a rapid grower that last September a series of measurements were made, at the suggestion of Dr. G. J. Peirce, in order to obtain some definite results. The lengths in the column under September are the measurements made September 25, 1903; those under May were made May 5, 1904, an interval of seven months and ten days. The winter rains did not begin for nearly two months after the measurements were made, and ceased two or three weeks before the lichens were remeasured, so that most of the growth was confined to a period of about five months. During the late winter and early spring growth must have been both rapid and continuous, since for nearly two months it rained almost daily, the temperature also being favorable for growth.

The thallus was measured from the point of attachment, the lobes measured being marked by a knot of silk thread, the weight of which was so inconsiderable as to have no effect on the growth. The measurements

[1] Synopsis N. A. Lichens, part 1, p. 22.

were of two kinds, the entire thallus, and individual lobes (*fig. 1*). To obtain the best results they should all be of the latter kind, as owing to the constant breaking off of long plants it is impossible to be sure of results, or even to find the plants measured. About twenty-five measurements were thus lost because the mistake was made of measuring the whole plant, which later was broken up by the winter rains and winds.

| Number | September | May | Growth | Per cent. of growth |
|---|---|---|---|---|
| 116 ............. | 3.0 cm | 4.1 cm | 1.1 cm | 36.66+ |
| 8218 A ........... | 34.0 | 38.0 | 4.0 | 11.76+ |
| B ........... | 6.0 | 7.5 | 1.5 | 25.00 |
| C ........... | 6.0 | 8.8 | 2.8 | 46.66+ |
| 96 A ........... | 28.0 | 32.5 | 4.5 | 16.07+ |
| B ........... | 16.0 | 25.0 | 9.0 | 56.25 |
| C ........... | 8.0 | 10.0 | 2.0 | 25.00 |
| 6418 A ........... | 46.0 | 54.0 | 8.0 | 17.00+ |
| B ........... | 47.0 | 90.0 | 43.0 | 91.00+ |
| 6505 A ........... | 5.0 | 7.3 | 2.3 | 46.00 |
| B ........... | 8.0 | 11.3 | 3.3 | 41.25 |
| C ........... | 3.5 | 5.3 | 1.8 | 51.42+ |

Dismissing no. 6418 B, which may be due to the tearing of the long thallus by the winds, we see that the short lobes, 3 to 16 cm in length, show a rate of growth astonishing for lichens; but one to be expected where they grow under such favorable conditions. Taking those fronds of 16 cm or less in length, we find an average growth in length of 41 per cent. No measurements were made to ascertain the increase in width of the lobes.

It was intended to make an extended series of measurements on various lichens, but it was not possible to do so. However, measurements were made of a specimen of *Parmelia caperata* (L.) Ach. growing on the trunk of *Aesculus californicus*.

| No. 5888 | September 25 | May 5 | Growth |
|---|---|---|---|
| Longitudinal diameter......... | 22.5 cm | 24 cm | 1.5 cm |
| Transverse diameter ......... | 21.0 | 22 | 1.0 |

The growth of this plant is really much greater than appears, as it is diffused over the entire margin of the circular thallus, and hence is difficult to express in percentages.

It is hoped that students in favorable localities may be induced by the above notes to undertake a series of measurements and observations on not only the very large foliaceous lichens, but also on the crustaceous lichens, many of which no doubt grow very rapidly.—ALBERT C. HERRE, *Stanford University, California*.

# CURRENT LITERATURE.

## BOOK REVIEWS.

### Flowering plants and ferns.[1]

Mr. J. C. Willis has done a wise thing in organizing his manual in a single volume. It is a book of general reference for those interested in learning something of the plants they meet in a botanical garden or museum, or in the field. In this edition much new material has been incorporated, especially in connection with those subjects that have had large recent development. The range of subjects covered is extraordinary, for the book gives the outlines of morphology, physiology, ecology, classification, geographical distribution, and the economic uses of vascular plants, besides containing "a dictionary in which the whole of the families and the important genera of flowering plants and ferns are dealt with."

It would seem impossible for one man to present such a range of subjects with any uniformity. He is almost sure to enlarge those he knows best at the expense of those with which he is the least familiar. For example, in this volume, while the older morphology with its copious terminology has full swing, the modern morphology has a scant showing and is presented in such a way as to bring no clear conception to the uninstructed. The alternation of generations and the various important evolutionary lines can be apprehended clearly only as they are approached by way of the lower plants. We have never seen any special gain in including these subjects in a book for the general reader dealing only with the vascular plants. If the statements are understood, they are not exact; and if they are exact, they cannot be understood.

These subjects, however, are very minor matters in the book, while the treatment of geographical distribution, forms of vegetation, and plant associations is extended and full of information. Mr. Willis seems to be more than anything else an ecologist, and his contact with various plant conditions has been unusual. As a consequence, this part of this book has all the flavor of personal experience.

The larger part of the volume is devoted to the presentation of the "classes, cohorts, orders, and chief genera," and is unique in the alphabetical arrangement and in the amount and kind of information one can find about plants concerning which he may be curious.

The book will certainly be of great use as a reference book in providing that kind of information for which it really stands, and the only adverse criticism is directed against its claim to include great regions of botany for which it does not stand.—J. M. C..

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[1] Willis, J. C., A manual and dictionary of the flowering plants and ferns. Second edition, revised and rearranged in one volume. Cambridge Biological Series. Pp. xii+670. Cambridge: The University Press. 1904.

### Vegetation of the Sihl valley.

A PORTION of the Sihl valley about $8^{km}$ south of Lake Zürich, Switzerland, is soon to be converted into a reservoir which will have an area of about $12^{sq\ km}$. This valley is celebrated botanically as the home of a number of rare species, and presents ecological conditions which have caused many unique features in the vegetation, particularly those which make this one of the most southern localities for a truly boreal moor-formation. As the most peculiar portions of the present vegetation will be completely destroyed and the surrounding regions consideralby modified, an important service has been rendered to science by Dr. Max Düggeli in the presentation of a complete ecological and floristic study of the present vegetation.[2] The completeness and care with which this work has been done make adequate review difficult. Among the unique features of the vegetation is the conifer forest (*Picea excelsa*) in the lowlands at an elevation which is characterized everywhere else in Switzerland by deciduous forests. The deciduous forests occur at higher levels along the valley slopes where there is better insolation, better drainage, and consequently warmer soil.

The most widespread formation in the trough of the valley is the low moor (*Flachmoor*), while in several small areas the high moor or sphagnum bog (*Hochmoor*) occurs. Many samples of peat were examined and the vegetable remains identified. These showed that no essential change has taken place in the vegetation since the last retreat of the ice, though remains of several species were found which do not now occur in the valley. Everywhere the samples showed that the low moor (Carex, Phragmites, Equisetum, Hypnum, etc.) is the pioneer, followed by the high moor (Sphagnum and its companions). The same succession was found in the horizontal series. The author considers the most important factor in determining the occurrence of low moor and high moor to be the amount of dissolved salts in the water. He contrasts these formations as follows. The low moor develops where the water comes from the earth charged with considerable mineral matter. It is flat and centripetal. The high moor on the other hand grows only in soft water nearly free from minerals, is raised at the center, and is centrifugal in development. Not until a considerable thickness of peat has accumulated can the sphagnum get a start in the low moor. To test his hypothesis that the mineral content of the water conditions the occurrence of the high moor, he staked out squares of sphagnum $30^{cm}$ on a side, and watered daily with a liter of water containing minerals. Sphagnum watered thus with water from the Sihl river was killed in eleven days. Solutions of $KNO_3$, $Na_3PO_4$, $MgCO_3$, $CaCO_3$, etc., gave a similar result. His solutions do not appear to have been made up on a very scientific basis, and he makes no mention of a control in which sphagnum is similarly treated with a mineral-free water, but the results are suggestive.

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[2] DUGGELI, MAX, Pflanzengeographische und wirtschaftliche Monographie des Sihltales bei Einsiedeln, von Roblesen bis Studen (Gebiet des projektierten Sihlsees). 8vo. pp. 222. *pls. 4. figs. 10.* Zürich: Zürcher & Furrer. 1903.

The numerous types of meadows are treated in an interesting manner. Besides giving a complete description of each type with its various modifications, he contrasts meadows differing only in the direction of the slope, and others differing only in the character of the soil, thus showing the great ecological significance of these factors.

There are many commendable features about the work which will make it a suggestive model for future studies of similar small areas, not the least important of these being the lucid literary style.—G. H. SHULL.

## NOTES FOR STUDENTS.

SHIBATA[1] proposes to designate as *amidases* certain enzymes found in the mycelium of *Aspergillus niger*, which spilt off ammonia from urea, biuret, and certain acid amides. They have nothing in common with the proteolytic enzymes. —C. R. B.

CHARLOTTE TERNETZ[2] finds in peat and peaty soils at least one fungus which is capable of fixing free N from the air. The fungus has a much branched septate mycelium and forms brown pycnidia which contain very small hyaline spores. It acts less energetically but more economically than *Clostridium Pasteurianum.*—C. R. B.

LIGNIER,[3] in an interesting comparison of the structures of Equisetales and Sphenophyllales, and of both with the structures of other pteridophytes, reaches the conclusion that these two groups, although differing in certain important particulars, really form one group, for which he proposes the name "Articulées." He further concludes that all the "Articulées" have a common ancestry, which was probably the most ancient Filicineae.—J. M. C.

LIGNIER[4] has discussed the nature of the so-called "flowers" of Gnetales in relation to similarly named structures in other gymnosperms and in angiosperms. He concludes that the staminate "flower" of Gnetales is a simple flower, and does not differ essentially from the much reduced flower of angiosperms; but that the ovulate "flower" is a very complex structure, really representing an inflorescence excessively reduced and condensed, and therefore could not be considered as a stage between the other gymnosperms and the angiosperms.—J. M. C.

IKENO, in reviewing and discussing the literature of the blepharoplast,[5]

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[1] SHIBATA, K., Über das Vorkommen von Amidespaltenden Enzymen bei Pilzen. Zeits. Ges. Biochemie **5**:384–394. 1904.

[2] TERNETZ, CHARLOTTE, Assimilation des atmosphärischen Stickstoffs durch ein torfbewohnenden Pilz. Ber. Deutsch. Bot. Gesells. **22**:267–274. 1904.

[3] LIGNIER, O., Equisétales et Sphénophyllales. Leur origine filicinéenne commune. Bull. Soc. Linn. Normandie V. **7**:93–137. 1903.

[4] LIGNIER, O., La fleur des Gnétacées est-elle intermédiaire entre celle des gymnospermes et celle des angiospermes? Bull. Soc. Linn. Normandie V. **7**:55–71. 1903.

[5] IKENO, S., Blepharoplasten im Pflanzenreich. Biol. Centrabl. **24**:211–221. *figs. 3.* 1904.

reasserts his previous view that the blepharoplast is a centrosome. He draws the following homologies between the structures concerned in plants (Characeae, Filicineae, and Equisetum) and animals (salamander and mouse): cilia are homologous with flagella; the thread from which the cilia are developed is homologous with the middle piece; and the deeply staining body in the plant spermatid (*Nebenkern* of Belajeff) is homologous with the deeply staining body (*Körperchen*) in the spermatid of animals.—CHARLES J. CHAMBERLAIN.

IN THE NUCLEI of the proembryo of *Ginkgo biloba*, according to ARNOLDI,[6] the chromatin is very inconspicuous, but increases in staining capacity and is easily seen during later stages in the development of the embryo. The staining reactions of the chromatin favor FISCHER's theory that staining reactions are due to physical rather than to chemical causes. After the embryo has become somewhat elongated, it is differentiated into an upper haustorial region, a middle region, which is the suspensor, and an apical region which gives rise to the embryo proper.—CHARLES J. CHAMBERLAIN.

LAURENT[7] has published the results of a study of the Juncaceae, the first part dealing with the phenomena extending from the first appearance of the ovule to the formation of the testa, the second part describing the phenomena connected with seed germination. Various species of Juncus and Luzula were used. The facts of pollination and of fertilization are as usual; the undifferentiated embryos of certain species of Juncus are in contrast with the completely organized embryos of Luzula; the suspensor "contributes" to the formation of periblem and forms the root cap; the antipodal tissue, especially in Luzula, is noticeably active; and the structure of the testa forms the basis of a division of Luzula into two groups. —J. M. C.

SCHRÖDER CONTRIBUTES further data on the statocyst theory of geotropic perception.[8] He has investigated a considerable number of plants in which the occurrence of mobile starch has been hitherto questionable. In all cases when the parts were geotropically sensitive (he examined many species and various parts) he found starch-bearing cells which may be considered statocysts in HABERLANDT's sense. A special study, also, was made of both stems and rhizoids of Chara. His results strengthen HABERLANDT's view that the *Glanzkörper* at the apex of the rhizoids act as statoliths, but he could find no such bodies in the shoots. He leaves unsettled the question as to whether the oil drops in the sporangium of *Phycomyces nitens* act as inverse statocysts.—C. R. B.

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[6] ARNOLDI, W., Beiträge zur Morphologie der Gymnospermen. VI. Ueber den Bau der Zellkerne im Embryo von *Ginkgo biloba*. VII. Die Embryobildung bei *Ginkgo biloba*. Ann. Inst. Agronomique et Forestière à Nowo-Alexandria **16**:1–22. 1903.

[7] LAURENT, MARCELLIN, Recherches sur le développement des Joncées. Ann. Sci. Nat. Bot. VIII. **19**: 97–192. *pls. 1–8.* 1904.

[8] SCHRÖDER, H., Zur Statolithentheorie des Geotropismus. Beihefte Bot· Centralbl. **16**: 269–288. *pl. 13.* 1904.

and four bracing extensions running downward and away from the track, nearly to the base of the high grade (*fig. 1*). The riprap wall, running parallel to the roadbed and $1.2^m$ below it, is $60^m$ long, varies from 1.5 to $2.5^m$ in perpendicular height, and rises at an angle of 45 to $55°$. The four bracing extensions run down the sides of the grade at right angles with the wall above and at an angle of about $30°$. The length of the extensions averages about $21^m$, and they vary from 2 to $2.7^m$ in width. A grass-sedge swamp lies to the north of the



Fig. 1.—View of a portion of the northward-exposed wall and portions of two of the extensions, showing something of the spermatophytic flora and the general plan of structure of the riprap.

society and contains a considerable amount of water in wet seasons. The vertical height of the grade above the swamp level is about $12^m$, and the riprap extensions pass from within $1.2^m$ of the track bed, downward to within $3^m$ of the swamp level. The riprap was built in 1874 and is thus thirty years old.

## II. ECOLOGIC FACTORS.

The conditions as a lichen-bearing substratum are unique in a number of ways. Though the same rocks used for walls under buildings and ten or more years older are apparently sound, the loosely

formation of the pollen is normal, a reduction in the number of chromosomes taking place in the pollen mother-cells. In the formation of the megaspore in some cases a tetrad of four megaspores is formed, accompanied by a reduction in the number of chromosomes. In other cases no reduction takes place in the megaspore mother-cells, and sometimes a true tetrad is not formed. Such conditions are not unexpected, since OVERTON had previously shown that while Thalictrum is often parthenogenetic fertilization may occur. The number of chromosomes in the sporophyte is twenty-four and in the gametophyte twelve. —CHARLES J. CHAMBERLAIN.

PARTHENOGENESIS in *Gnetum Ula* Brogn. is reported by LOTSY.[15] In the development of the female gametophyte, as in *G. Gnemon*, a period of free nuclear division is followed by a period of cell formation. The cells of the lower part of the gametophyte are small and form a close tissue, while in the upper part they are much larger and are loosely associated. No pollen tubes were observed, but many of the loose cells in the upper part of the gametophyte behaved like zygotes, sending out tubes as described for other species of Gnetum. The number of cells behaving in this way was so large that the pollen tubes could scarcely have been overlooked had they been present. This study has strengthened LOTSY in his previous view that the angiosperms have not come from the Gnetaceae.—CHARLES J. CHAMBERLAIN.

CARLETON[16] has published a series of notes giving the results of investigations and culture experiments with rusts. It is found that *Uromy es euphorbiae* can be propagated through the agency of seeds and seed pods infected with the fungus. This is the first instance of a rust propagated in this manner. A long series of experiments with the black stem rust of Agropyron and Elymus showed that this rust could be transferred to a number of hosts, including wheat, barley, *Hordeum jubatum*, *Agropyron tenerum*, *A. Richardsoni*, *Elymus canadensis;* while the orange leaf rust of the same species is sharply limited in its host plants. The fact mentioned by the writer in a former paper, that the uredo of the orange leaf rust is hardy during the winter, is again emphasized in this discussion. It is also shown that the uredo of blue grass rust is hardy.—H. HASSELBRING.

THE FACT that copper sulfate is much more toxic in its effect upon plants than upon animals is taken advantage of by MOORE and KELLERMAN[17] in a method for killing algae, etc., in reservoirs, without at the the same time rendering the water injurious for human consumption. According to the organisms to be exterminated, to the flow of the water, and other conditions, a certain amount of the poison is added to the reservoir, a device being used to insure uniform

[15] LOTSY, J. P., Parthenogenesis bei *Gnetum Ula* Brogn. Flora **92**: 397–404. *pls. 9–10.* 1903.

[16] CARLETON, M. A., Investigations of rusts. U. S. Dept. of Argic. Bur. Pl. Indus. Bull. 63. pp. 29. *pls. 2.* 1904.

[17] MOORE, G. T., and KELLERMAN, K. F., A method of destroying or preventing the growth of algae and certain pathogenic bacteria in water supplies. U. S. Dept. of Agric. Bur. Pl. Indus. Bull. 64. pp. 44. 1904.

distribution of the salt. The amount of copper salt needed will never exceed one part in a million of water, and since copper is not poisonous to human beings in doses of less than perhaps $0.02^{gm}$ daily, it appears that some fifty quarts of treated water might be taken daily with impunity! The paper represents what seems to the reviewer to be a most excellent piece of work.—B. E. LIVINGSTON.

ROLFS[18] has described several diseases of citrous trees and fruits due to *Colletotrichum gloeosporioides*. When the fungus attacks the young growing twigs, into which it gains entrance through the leaves, it produces a disease known as "wither-tip," characterized by the dying back of the young branches. The most serious damage is caused to the mature fruit into which the fungus gains entrance through an injury or bruise. The fungus rapidly develops until the whole rind is brown. This injury occurs to a large extent during the handling of the fruit, especially in the coloring process. All varieties of citrous fruits are attacked by the fungus. Spraying with potassium sulfid and copper mixtures are suggested as remedies, although no experimental data are given. Cultivation, fertilization, and pruning are also suggested as preventive measures. — H. HASSELBRING.

A RECENT CONTRIBUTION[19] from the Gray Herbarium contains six papers by the various members of the herbarium staff. The first three, by B. L. ROBINSON and J. M. GREENMAN, are "Revision of the genus Sabazia," chiefly Mexican in distribution and containing 6 species; "Revision of the Mexican and Central American species of Trixis," 16 species being presented, 6 of which are new; and "Revision of the Mexican and Central American species of Hieracium," 5 of the 19 species being new. The two papers by M. L. FERNALD are "Synopsis of the Mexican and Central American species of Alnus," one of the six species being new; and "Some new species of Mexican and Nicaraguan dicotyledons," 13 being described. A paper by J. M. GREENMAN, entitled "Diagnoses and synonymy of Mexican and Central American spermatophytes," includes descriptions of 39 new species, besides new varieties and discussions of certain critical species.—J. M. C.

HYBRIDS between Fundulus and Menedia have been investigated by MOENKHAUS.[20] The fertilized eggs begin to develop normally, but abnormalities soon appear and the embryos do not develop beyond the closure of the blastopore. Botanists will be interested in the history of the chromatin. The chromosomes of Fundulus are rather long and straight, while those of Menedia are shorter

[18] ROLFS, P. H., Wither tip and other diseases of citrous trees and fruits caused by *Colletotrichum gloeosporioides*. Bur. Pl. Industry, Bull. 52. pp. 20. *pls. 6.* 1904.

[19] Contributions from the Gray Herbarium of Harvard University. N. S. no. XXVIII. Proc. Amer. Acad. Sci. **40**: 1–57. 1904.

[20] MOENKHAUS, W. J., The development of the hybrids between *Fundulus heteroclitus* and *Menedia notata* with especial reference to the behavior of the maternal and paternal chromatin. Amer. Jour. Anat. **3**: 29–65. *pls. 1–4.* 1904.

and are usually curved; consequently it is possible to distinguish the paternal and maternal chromosomes during fertilization and during mitosis. At the first two mitoses in the fertilized egg the two chromatins appear grouped and bilaterally arranged on the spindle, but later the grouping disappears. There is a mingling of chromatin in the resting nuclei, but the characteristic chromosomes of the two parents can be distinguished during mitosis. The writer strongly supports the theory that the chromosome is a permanent organ of the cell.—CHARLES J. CHAMBERLAIN.

THE THEORY of the individuality of the chromosome is supported in a recent paper by ROSENBERG,[21] whose work on Drosera has already furnished considerable evidence in favor of this view. In the resting nuclei of Capsella, particularly in the nuclei of the cells of the suspensor, the 32 chromosomes characteristic of the species can be counted without difficulty. The same number was counted in the sporophytic mitoses, and 16 were counted in the pollen mother-cells and in the embryo sac. Further, 48 were found in mitosis in the endosperm. Mitoses in Zostera show 6 chromosomes in pollen mother-cells and 12 in root tips. Resting nuclei in the seed coat showed 12 chromosomes. Resting nuclei in the integument of Calendula showed about 30 chromosomes, while mitoses showed 32 in the sporophyte and 16 in the gametophyte. The forms mentioned have short thick chromosomes, which are more easily traced into the resting condition of the nucleus than are the long filamentous chromosomes of the Fritillaria type. —CHARLES J. CHAMBERLAIN.

LEAVITT[22] has published the results of an extensive study of root hairs. Two types are recognized. In one case any cell of the piliferous layer in the young fixed tissue may produce a hair, there being no specialization for this purpose. This type is characteristic of most Filices, of some monocotyledons, and of the dicotyledons. In the other case special cells for producing hairs are cut off in the very young piliferous layer by a peculiarly oriented cell-division. These specialized cells the author calls "trichoblasts," and they are characteristic of all pteridophytes except most Filices, of most monocotyledons, and of the Nymphaeaceae among the dicotyledons. Attention is also called to the relationship in origin, form, and probable function between the trichoblasts and the so-called "transfusion cells" of the hypodermal layer, the short roundish or oval cells that alternate in each longitudinal row with the elongated prismatic ones. It is singular that among other references to literature the author has not included his own paper[23] of two years ago, in which the trichoblasts of Azolla were fully described. —J. M. C.

[21] ROSENBERG, O., Ueber die Individualität der Chromosomen im Pflanzenreich, Flora **93**: 251–259. *figs. 7.* 1904.

[22] LEAVITT, R. G., Trichomes of the root in vascular cryptogams and angiosperms. Proc. Boston Soc. Nat. Hist. **31**:273–313. *pls. 16–19.* 1904.

[23] The root hairs, cap, and sheath of Azolla. BOT. GAZ. **34**:414–419. *pl. 16.* 1902.

THE FORMATION of the heterotypic chromosome is described in a recent article by BERGHS.[24] Although referring often to a "longitudinal division" of the spirem, the writer wishes it understood that he means merely the appearance throughout the length of the spirem of two filaments more or less parallel. Whether the two filaments result from the splitting of a single filament or whether there is simply the reappearance of two distinct filaments will be discussed in a future paper. The split which appears in the spirem is the one which separates the two filaments entangled in the strepsinema stage. The spirem passes into the strepsinema stage by a longitudinal fission, not by looping and approximation, as DIXON claims. After the strepsinema stage, the chromosomes are completed by a thickening and shortening. The two pieces, which the heterotypic mitosis separates, are the two longitudinal pieces of the spirem thread. If there is an approximation, it must be looked for during the formation of the spirem· This latter point will be discussed in a forthcoming paper.—CHARLES J. CHAMBERLAIN.

ROSENBERG,[25] in continuing his studies upon *Drosera rotundifolia*, describes the two mitoses in the pollen mother-cells and arrives at some interesting conclusions. In an early prophase of the first division, before the disappearance of the nuclear membrane, the chromosomes appear in pairs, which soon unite to form double chromosomes. There are 20 such double chromosomes, and they are formed by the uniting of the 40 chromosomes of the vegetative mitoses. In a series of diagrams the paternal and maternal chromosomes are represented first as distinct, and soon after as approximated in pairs. Each paternal and maternal chromosome now divides, and all of the paternal chromosomes pass to one pole and all of the maternal to the other pole. The second mitosis simply separates the two parts of each chromosome, which was already formed during the prophase of the first division, so that in two of the four pollen grains all of the chromosomes are paternal and in the other two, all are maternal. The suggestion is made that the double thread of the early spirem is due to fusion rather than to splitting, and is consequently a process of reduction.—CHARLES J. CHAMBERLAIN.

TWO PAPERS from the University of St. Petersburg bear upon the rôle of enzymes in respiration. Both are based upon quantitative work.

KOSTYTSCHEW[26] experimented with *Mucor stolonifer* and *Aspergillus niger*.

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[24] BERGHS, JULES, La formation des chromosomes heterotypiques dans la chromosome végétale. I. Depuis le spirème jusqu'aux chromosomes mûrs dans la microsporogénèse d' *Allium fistulosum* et de *Lilium lancifolium* (*speciosum*). Le Cellule 21: 173–189. *fig. 15.* 1904.

[25] ROSENBERG, O., Ueber die Reduktionsteilung im Drosera. Meddel. Stockholms Högs. Bot. Inst. pp. 13. *figs. 20.* (Reprint signed April 1904, but the volume and date of the publication in which the article appeared are not indicated.)

[26] KOSTYTSCHEW, S., Über Atmungsenzyme der Schimmelpilze. Ber. Deutsch. Bot. Gesells. 22:207–215. 1904.

His most important conclusions are that both the absorption of oxygen and the excretion of carbon dioxid in the respiratory process are at least partially effected by the activity of specific enzymes; and that the excretion of carbon dioxid when free oxygen is excluded is occasioned by the activity of an enzyme which is not identical with the zymase of BUCHNER.

MAXIMOW[27] studied the behavior of the liquor expressed from the mycelium of *Aspergillus niger*, and obtained the important result that this liquor on standing exhibits a gas metabolism analogous to respiration. This exchange of gases occurs as a consequence of the activity of enzymes present in the liquor. The excretion of carbon dioxid is accomplished by an enzyme analogous to zymase, while the absorption of oxygen is induced by one of the oxydases. The former enzyme analogous to zymase also resembles zymase in being equally active in air or in hydrogen.—R. H. POND.

SABLINE[28] subjected roots of *Vicia Faba* to different temperatures; to lack of oxygen; to the action of saccharose, distilled water, sulfuric ether, quinin sulfate, and lithium chlorid, in order to determine the effect of various conditions on karyokinesis. Few divisions were found in roots subjected to 0° C. The linin was coarse-meshed and the chromatin stained blue. At 10° growth was slow and chromosomes blue. At 30°, the optimum temperature, the nucleoli did not wholly disappear in some instances, and the chromosomes stained blue; when the nucleoli disappeared the chromosomes stained red. After deprivation of oxygen chromosomes stained red. When subjected to saccharose the chromosomes were very large and stained red, and nucleoli were enormous. There were no mitoses in cells placed in distilled water. Amitosis was frequent in nuclei subjected to the action of sulfuric ether. In nuclei which divided mitotically the chromosomes were frequently scattered, and in some cells stained red, in others blue. Amitotic division was sometimes found in cells acted on by quinine sulfate. Multipolar spindles were frequent. Lithium chlorid caused the chromosomes to become abnormally large and the stain was red.—W. J. G. LAND.

A PAPER from Pfeffer's laboratory by WIEDERSHEIM[29] contributes new data to the physiology of photonastic and thermonastic movements. The opinion of JOST and SCHWENDENER that only the primary movement in response is a direct result of external stimulation, while the secondary movement constituting a correction of the primary movement is autotropic, is not supported. The view of PFEFFER that the secondary movement is not autotropic but is directly induced by the same stimulus which causes the primary movement, is strongly supported. The prophecy of FITTING that the "double curve" expressing the twice accel-

[27] MAXIMOW, N. A., Zur Frage über die Atmung. (Vorläufige Mitteilung). Ber Deutsch. Bot. Gesells. 22: 225–235. *fig. 1.* 1904.

[28] SABLINE, V., L'influence des agents externes sur la division des noyaux dans les racines de *Vicia Faba.* Rev. Gén. Bot. 15:481–497. *pls. 15, 16.* 1903.

[29] WIEDERSHEIM, W., Studien über photonastische und thermonastische Bewegungen. Jahrb. Wiss. Bot. 40:230–278. *figs. 20.* 1904.

erated growth of the "middle zone" which was found by him to characterize the haptotropic movements of tendrils could also be demonstrated for photonastic and thermonastic movements is entirely fulfilled. FISCHER'S assignment of *Impatiens parviflora* to the group of autonyctitropic plants is ratified. The plants best suited for investigation of photonastic movements were found to be *Impatiens parviflora, I. glanduligera,* and *Chenopodium album;* while *Tulipa Duc van Toll* and *Crocus luteus* are excellent for study of thermonastic movements. The conclusions are based upon data obtained by the quantitative methods which characterize the laboratory in which the investigation was made.—RAYMOND H. POND.

A SUGGESTION as to the formation of asparagin is advanced by PRIANISCHNI-KOW[30] in a preliminary paper. He argues that as the decomposition of proteids tends to produce ammonia on the one hand, and amidoacids (perhaps even aspartic acid) on the other, asparagin may be produced by the formation of ammonium aspartate from which a molecule of water separates. This secondary origin of asparagin rather than its origination as a direct decomposition product of proteids he infers from the following facts.

He and others have found that the relative amounts of asparagin and aspartic acid produced in germination and by hydrolysis of proteids are quite unlike, and they are the more unlike the later the stage of germination. In late stages the rate of asparagin production even surpasses that of proteid decomposition. Further it has been found that the decomposition of proteids by proteolytic enzymes (such as occur in the germinating seeds) gives rise to the same amidoacids and bases as hydrolysis with mineral acids, but no asparagin is formed. Finally, the distribution of asparagin in the cotyledons and growing regions is not such as would occur were it produced for migration out of the stored proteids in the cotyledons, since it is much more abundant in the growing parts than in the cotyledons.—C. R. B.

GATIN[31] has been investigating the development of the first root in the germination of *Archontophoenix Alexandrae* and *Phoenix canariensis.* The first mentioned follows the "admotiva" mode of germination in which the hypocotyl scarcely elongates. *P. canariensis* follows the "remotiva" method, the hypocotyl elongating for the supposed purpose of burying the young plant. The mature embryo of *A. Alexandrae* possesses a root of which a rudimentary vascular axis only is present. The cortex arises during germination from a zone surrounding the tip of this axis and forming apparently an integral part of the cotyledonary tissue. The region lying directly in the path of growth of the vascular axis is distinguishable into three parts. The innermost, lying directly in contact with the end of the axis, forms the root-cap. The next, together with the adjacent

30 PRIANISCHNIKOW, D., Zur Frage der Asparaginbildung. (Vorläufige Mitteilung.) Ber. Deutsch. Bot. Gesells. **22**: 35–43. 1904.

31 GATIN, C. L., Observations sur la germination et la formation de la première racine de quelques palmiers. Rev. Gén. Bot. **16**: 177–187. *figs. 7.* 1904.

epidermis, which forms the outermost, enters into the formation of a root sheath. The first root forms an angle of about 90° with the axis of the shoot. A subsequently formed adventitious root, which continues the shoot axis, exceeds the primary in growth and becomes the principal root at least for a time. The origin of cortex, cap, and sheath in *P. canariensis* is the same as in *A. Alexandrae*, but the axis of the primary root coincides with that of the shoot, so that the first root remains the principal one.—F. H. BILLINGS.

GERASSIMOW[32] has investigated the influence of the nucleus on the growth of the cell. By exposing various species of Spirogyra with cells in the process of division for one-half an hour to one hour to a temperature a little above 0° C., he was able so to interfere with the processes of mitosis that the following irregularities arose when the filaments were transferred and cultivated under normal conditions: cells with a single large nucleus, the equivalent of two normal nuclei; cells with the daughter nuclei fused to a greater or less extent, giving one the impression of amitosis; cells in which the daughter nuclei are normally formed but lie close to one another and both on the same side of the newly formed cell wall. This wall is either complete, thus cutting off a cell without a nucleus, or a small opening remains forming a non-nucleate chamber communicating with a binucleate cell. From a large number of measurements made upon cells as above described the author draws the following conclusions: the growth of the cells having an excess of nuclear material is greater than the average growth of normal cells; the non-nucleate cells are short-lived and the growth is very slight; the non-nucleate chambers are longer-lived and grow more than the non-nucleate cells; the cells having an excess of nuclear material may conjugate either with normal cells or with cells similar to themselves.—C. F. HOTTES.

ZIMMERMANN[33] has described the most important insects and fungous enemies of the coffee plant in the Island of Java. The following are noted here for reference. A sort of stigmonose is produced by punctures of *Pentatoma plebeja*, which attacks the lower side of the leaves and young stems. The author was unable to observe any detrimental effect on the plant due to punctures on the leaves. Very young shoots, however, wither as a result of the insect punctures. The histological characteristics of the punctures are described in detail. Of the fungi described, the well-known *Hemileia vastatrix*, occurring everywhere on the island each season, causes the greatest loss. This rust fungus is often accompanied by other parasites, as *Gloeosporium coffeanum* Del., *Coniothyrium coffeae* Zimm., *Colletotrichum incarnatum* Zimm., and *Cercospora coffeicola* Berk. & Cooke. *Capnodium javanicum*, *Rhombostilbella rosea*, and *Antennaria setosa* are described as new species growing on the surface of the leaves in secretions of *Lecanium viride* and other insects. A fungus whose systematic position is not

32 GERASSIMOW, J. J., Zur Physiologie der Zelle. Bull. Soc. Imp. Nat. Moscow. no. 1, pp. 134. *pl. 1.* tables 60. 1904.

33 ZIMMERMANN, A., Einige pathologische en physiologische Waarnemingen over Koffie. Mededel. 's Lands Plantentuin, no. 67. pp. 105. *pls. 4.* 1904.

certain causes an injury termed "spiderweb disease." A number of other fungi, many of them new, are described on the stems, roots, and fruit of the plant. Those on the fruit are mostly saprophytic molds. The last part of the report contains some observations on sterility of coffee flowers, variation in the fruit, polyembryony and the influence of light, and injuries due to nematodes.—H. HASSEL-BRING.

THE INFLUENCE of chloral hydrate upon nuclear and cell division is described in a recent paper by NĚMEC.[34] It is possible that very weak solutions may stimulate division, but more concentrated solutions cause various disturbances. Some stages in mitosis are more readily and more profoundly influenced than others. The phragmoplast is most resistant. The stages of metakinesis are much less resistant, and the equatorial plate stages and stages in the formation of the spindle are the most sensitive of all. Root tips which have been treated for an hour in 0.75 per cent. chloral hydrate show a degeneration of the spindle fibers and an interruption of mitosis. If the solution be washed out and normal conditions restored, mitosis proceeds in the usual manner, but the interrupted mitoses give rise to cells with several nuclei, or an irregular nucleus and incomplete walls may be formed. In binucleate cells the nuclei may fuse, and the nucleus resulting from such a fusion has double the usual number of chromosomes. In cells in which the two nuclei do not fuse, two mitoses may occur simultaneously. Cells without nuclei may be formed. Mitoses with double the number of chromosomes gradually disappear from the root tip and apparently a reduction in the number of chromosomes takes place. There was no conclusive evidence that chloral hydrate causes amitosis. Figures which might be mistaken for amitosis were abundant, but they could be interpreted as interrupted or modified mitoses. —CHARLES J. CHAMBERLAIN.

NON-SEXUAL NUCLEAR FUSIONS is the title of a series of short papers by NĚMEC.[35] Much of the material was obtained by treating root tips of seedlings of *Pisum sativum* with a 0.75 per cent. solution of chloral hydrate. Tips 3 to 3.5$^{cm}$ long were placed about 2$^{cm}$ deep in the solution and allowed to remain for an hour. They were then washed in water, material being fixed at intervals. Material fixed immediately after removal from the chloral solution shows numerous binucleate cells besides other abnormalities. After an hour's washing in water normal mitosis and abnormalities become less numerous, and after about twenty-eight hours' washing the processes are practically normal. The nuclei of the binucleate cells fuse and some stages in the fusion might be mistaken for amitosis. No amitosis, however, was observed. When a nucleus which has resulted from fusion divides, it shows double the number of chromosomes characteristic of the sporophytic cells. NĚMEC believes that the double number is not maintained

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[34] NĚMEC, B., Ueber die Einwirkung des Chloralhydrats auf die Kern und Zellteilung. Jarhb. Wiss. Bot. **39**: 645–730. *figs. 157.* 1904.

[35] NĚMEC, B., Ueber ungeschlechtliche Kernverschmelzungen. Sitz. Ber. Königl. Böhm. Gesells. Wiss. I, 1902; II, July 1903; III, Nov. 1903.

but soon becomes reduced.   The fusions resemble sexual fusions in the behavior of the chromatin.   The nuclear fusion and the reduction may be regarded as automatically regulated phenomena.   Reduction may sometimes be an atavistic character; it is a result of fusion rather than a preparation for it.   Morphologically the most important character of fertilization lies not in nuclear fusion but in cell fusion.   When the conditions for cell fusion are present the other phenomena (under certain conditions) follow necessarily as automatically regulated processes.—CHARLES J. CHAMBERLAIN.

THE EXTANT theories of causality in leaf arrangement have been critically discussed in detail by WINKLER[36] in two parts of a paper on this subject, of which we are promised a continuation in a third part.   The author brings forward evidence from various plants that the mechanical theory of SCHWENDENER will not suffice to explain the formation and development of primordia.   There appear to be many cases in which the primordia are not constant in size at the start, many in which contact or absence of contact between different primordia plays no controlling rôle in development, and also many in which pressure of older parts has no influence.   The various theories of teleological nature, such as the common one which attributes leaf arrangement to the need of having these organs so placed as to give best access of air and light, are discussed rather more fully than would seem necessary for intelligent readers.   It is to be hoped that such theories may at length be accorded a decent burial and then allowed to rest.

The constructive part of this paper points out that any theory of leaf arrangement which is satisfactory must consider internal factors together with the external ones.   WINKLER is careful to indicate that by this term he refers merely to those protoplasmic conditions (probably purely physical) of which we know absolutely nothing at present except that they exist.   The general conclusion of the paper may be summed up in a paraphrase of the author's words, that the formation of organs at the growing tip is an extraordinarily complex process controlled by a whole series of factors of different kinds, concerning the nature and influence of which we know practically nothing.—B. E. LIVINGSTON.

SWINGLE[37] has just published the results of his study of the date palm, and they are important not only in demonstrating the possibilities of a valuable crop for the United States in regions otherwise apparently hopeless from an agricultural point of view, but also from their much larger practical bearing upon the value of such investigations.   The following statement is vigorous, but who will dispute it ?   "At present it is no exaggeration to state that the life history requirements and the limits of the power to resist unfavorable environmental conditions are far better known for many microscopic lower plants, such as bacteria, fungi, and algae, even for species having no economic importance, than for the most

[36] WINKLER, H., Untersuchungen zur Theorie der Blattstellungen.   I.   Jahrb. Wiss. Bot. **36** : 1–79. *pls. 4.* 1901; II, *ibid.* 501–544. *pl. 1.* 1903.

[37] SWINGLE, W. T., The date palm and its utilization in the southwestern states, pp. 155. *pls. 22.*   Bur. Pl. Industry, U. S. Dept. Agric., Bulletin 53., April 28. 1904.

important crop plants whose culture provides employment for tens of millions, and whose products constitute the daily food of hundreds of millions of human beings. Such a condition is discreditable alike to biological and to agricultural science and should not longer continue."

In reference to the date palm the following conclusions are reached: It can endure any degree of heat and any amount of dryness in the air, and is even favored by hot winds and by a rainless summer. The best sorts can mature only in regions having a very long and very hot growing season. It can endure more alkali in the soil than any other profitable crop plant, and can thrive on soils containing from 0.5 to 1 per cent. of alkali, even when irrigated with brackish water containing 0.43 per cent. (430 parts per 100,000) or more of injurious alkali. It can withstand without injury accumulations of alkali at the surface of the soil that would kill all other crop plants, even those considered to be very resistant to alkali.—J. M. C.

PORSILD[38] gives an account of the expedition to Disko Island in 1898. The account includes observations on the geology and topography of the island, incidental notes on the fauna, and detailed notes on the flora. In conclusion he discusses the southern flora of the island, considering the questions of possible relict endemism from a warmer epoch, and migration in postglacial times.

The upland vegetation consists of lichens and herbaceous plants with very few shrubs. Under this category are placed the windy plateaus, the sheltered terraces of the trap, the gravelly bottoms and deltas, and the raised sea bottoms. The Calluna heath is found on the talus and gradual slopes of the trap, on large hills poor in humus, or in depressions rich in water. The tundra is discussed as a peculiar formation transitional between the moss-bog and the Calluna heath, the transition to one or the other depending upon the water content of the soil. Moss bogs are found where water stagnates and is sour, on gneiss, on uneven basalt, and on undrained terraces, where the bog often goes above the Calluna. In some cases the moss formation actually forms the climax type after the Calluna, and in comparison is relatively unmixed in its species.

Halophytes occur along the sea strand. Cyperaceous meadows occur only along streams in very flat and moist soil. Dwarf birches and willows are also found along streams, the former occurring on a somewhat drier soil than the latter.

As regards vegetation in the inland waters, lakes are poor in species, but rich in individuals. Glacial streams contain no vegetation or at most only a few diatoms. Other streams, especially the warm ones, are rich in algae, especially *Hydrurus foetidus*. The floristic difference on gneiss and basalt is not marked when flowering plants are considered. Mosses, on the other hand, decidedly prefer the one or the other. Thus species of *Andreaea*, *Sphagnum*, and *Sarcos-*

    [38] PORSILD, M. P., Bidrag til en Skildring af Vegetationen paa Öen Disko tilligemed spredte topografiske og zoologiske Iagttagelser. Meddel. om Grönland **25**: 91–308. *pls. 1–6.* 1902.

*cyphus* never occur on basalt or tuff, while *Drepanium, Thuidium abietinum, Brachythecium salebrosum,* and *Pottia latifolia* are characteristic basalt plants. —G. H. JENSEN.

IN A RATHER lengthy paper on embryonal substance, NOLL[39] discusses the various theories which have been announced regarding the controlling force in development, and presents some interesting observations on the protoplasm of the growing tip in Bryopsis, together with his interpretation of the latter. The facts, determined by very careful observation of the growing tips, are as follows: The protoplasmic circulation of the filament occurs throughout the whole plant, extending into the tip region as well as elsewhere; nevertheless the protoplasm of the apical portion is very different from that below. While the non-growing portions have only the usual thin protoplasmic layer lining the wall, that of the growing tip occupies the whole lumen. Also in the tip there are no chloroplasts, and the protoplasm is much more dense than elsewhere, while the nuclei are more numerous. Since the currents of cyclosis are constantly carrying new substance into the tip and out again, there is a constant transformation of protoplasm at the limit of the denser region from somatic to meristematic and *vice versa*. At this limit the entering substance becomes more dense and the chloroplasts are left behind in apparently somewhat the same way as lighter bodies float upon water. NOLL suggests that the increase in density may be due to loss of water from the entering protoplasm. (It occurs to the reviewer that it may be due to incipient coagulation of the colloidal bodies.)

On account of this constant interchange between apical and more basal portions, it is impossible to suppose here that the meristematic protoplasm in the former region is fundamentally different from the somatic. The author concludes that, since the *Hautschicht* is the only part of the living substance which is constantly at the tip, and does not take part in the cyclosis, it must be in this that the controlling factor of growth is located. Thus he looks upon the *Hautschicht* of the tip as the only true embryonal substance here, and it does not contain nuclei. Therefore, he points out that in Bryopsis the factor producing growth does not lie in nuclei. The objection to this conclusion lies in the fact that we cannot be sure that some form of cyclosis does not occur in the *Hautschicht;* that it is not observed does not prove its absence.—B. E. LIVINGSTON.

SPERMATOGENESIS in *Marchantia polymorpha* has been reinvestigated by IKENO.[40] In many points this investigation has confirmed the earlier work of STRASBURGER and SCHOTTLÄNDER, but the more critical methods have made it possible to bring out important features which have hitherto been overlooked. During the early divisions in the young antheridium no nucleolus is demonstrated; the number of chromosomes is eight, as SCHOTTLÄNDER has already shown.

39 NOLL, F., Beobachtungen und Betrachtungen über embryonale Substanz. Biol. Centralbl. **23**: 281–297, 321–337, 401–427. 1903.

40 IKENO, S., Die Spermatogenesis von *Marchantia polymorpha*. Beih. Bot. Centralbl. **15**:65–88. *pl. 3.* 1903.

SCHOTTLÄNDER'S statement that centrosomes are present during the diaster and dispirem stages in young antheridia is also confirmed. Centrosomes were found throughout the spermatogenous divisions, during which they perform the ordinary functions of centrosomes. They do not persist throughout the life history of the cell, but appear at the beginning of each mitosis and disappear by the time the dispirem stage is reached. After the spermatogenous divisions have ceased, the centrosome reappears, functioning not as a centrosome but as a blepharoplast giving rise to the cilia. IKENO interprets as genuine centrosomes the blepharoplasts of various pteridophytes and of the cycads and Ginkgo.

According to current accounts, the spermatogenous tissue, at the close of the spermatogenous divisions, consists of approximately cubical sperm mother-cells, each of which gives rise to a single spermatozoid. The present investigation shows that there is still another nuclear division in a diagonal plane and not followed by the formation of a cell wall, so that each sperm mother-cell gives rise to two spermatozoids. This is true not only for Marchantia, but probably for other liverworts also. At this diagonal division, the centrosomes, after functioning as centrosomes, do not disappear, but persist and function as blepharoplasts. The blepharoplast elongates, and its body comes into close contact with the inner surface of the spermatid cell, so that it appears like a thickening of the *Hautschicht*. From this elongated centrosome, or blepharoplast, come the two cilia.

Shortly after the diagonal division a peculiar spherical body, staining somewhat like the centrosome, appears in each spermatid mother-cell, but is readily distinguished from the centrosome by its larger size and its position. It is still distinguishable after the centrosome has given rise to the cilia. From the resemblance to the chromatoid body of some animals, the same name is suggested for this body. Occasionally each of the cells resulting from the diagonal division divides. Such a division is accompanied by a division of the chromatoid body and of the centrosome. Thus four spermatozoids would be formed from what is usually denominated a sperm mother-cell. However, only two spermatozoids mature, the supernumerary ones being used for nutrition. This homology of the centrosome is fully discussed.—C. J. CHAMBERLAIN.

PROBLEMS CONCERNING WATER ABSORPTION by epiphytic Bromeliaceae have been investigated by MEZ,[41] who has gone carefully over the ground traversed a few years ago by SCHIMPER. He agrees with SCHIMPER in most particulars, but is at variance with him regarding the behavior of the individual scale during water absorption. SCHIMPER claimed that the four central and empty cells of the shield part of the scale are filled with air when the surface of the plant is dry, and that the air is replaced by water when the surface is wet. MEZ by microchemical tests, as well as by direct observation, finds that the cavities of

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[41] MEZ, CARL, Physiologische Bromliaceen-Studien. I. Die Wasser-Oekonomie der extrematmosphærischen Tillandsien. Jahrb. Wiss. Bot. **40**: 157–229. *figs. 26.* 1904.

the four cells are always free from air, so that when dry conditions prevail they are in a state of complete collapse. The much thickened upper surface of the shield part, or *Deckel*, is the active part concerned in absorption of water from the capillary spaces beneath the scale. It is composed of a mesh of cellulose containing large deposits of pectin. A layer of pure cellulose covers all. When wet, this *Deckel* absorbs water rapidly, and being resisted beneath by the epidermis, as well as on the sides by the cellulose wing of the scale, the only direction in which swelling can take place is upwards. As a consequence, the *Deckel* becomes convex, the cone-like processes on its under side straighten out and become more obtuse, with the result that the collapsed walls of the four cells separate, causing cavities into which water is drawn through thin areas in their outer walls, in response to the negative pressure. Water is thus absorbed till the scale is distended to its greatest extent, and the four central cells are filled with water. MEZ has calculated the amount thus drawn into one scale in *Tillandsia streptocarpa*, and found it to be approximately $0.000464^{cu\ mm}$ or $1.451^{cc}$ for a given entire plant having 1,880,000 scales. The shield, or central region of the scale, lies in connection with a row of 1–4 living cells, which in part form the stalk of the scale. The uppermost of these is larger than the others and borders directly on the four water-filled cells. The transverse walls of this cell are cuticularized except in certain small areas. The water contained in the four cells adjacent above is drawn through these areas into the cell by osmotic action due to the presence of sugar in the cell sap.

The water is passed on through the series of stalk cells, whose cross walls have uncuticularized areas, till the mesophyll is reached. This continues till the water in the capillary spaces outside is exhausted, or until the plant is supplied. The water remaining in the four central shield cells is not available to the plant, as the tension of the scale overbalances the absorptive power due to osmosis. This water must pass off by evaporation from the surface of the scale. It will be seen that the scale acts like a suction pump in drawing water into the cells, whence it may be absorbed into the plant by the usual process of osmosis.—F. H. BILLINGS.

ITEMS OF TAXONOMIC INTEREST are as follows: H. and P. SYDOW (Ann. Mycol. 2:162–174. 1904), among descriptions of many new species of fungi, establish *Microcyclus*, *Phaeodothis*, and *Maurodothis* as new genera of Dothideaceae.—E. L. GREENE (Ottawa Nat. 18:37–39. 1904) in a second paper on Canadian Antennarias describes five new species.—T. S. BRANDEGEE (Zoe 5:179–182. 1904) has described new Mexican species of Thelypodium (2), Spermacoce, Gentiana, Gilia, Castilleia, and Krynitzkia.—J. M. GREENMAN (*ibid.* 183–187) has described new species of Cerastium (3), Arenaria, Dalea, Nama, and Eupatorium (2) from Mexico.—KATHARINE BRANDEGEE (*ibid.* 189–194), among other critical notes on Cactaceae, has described new species of Cereus (4) and Mammillaria (2).—L. DIELS and E. PRITZEL (Engler's Bot. Jahrb. 35:55–160. 1904), under the title "Fragmenta Phytographiae Australiae occidentalis," present

a list of the plants through Proteaceae, with critical notes, including descriptions of new species and the following new genera: *Dielsia* Gilg (Restionaceae) and *Hydatella* Diels (Centrolepidaceae).—KENNETH K. MACKENZIE (Torreya **4**:56–57. 1904) has described a new species of Œnothera from West Virginia.—D. R. SUMSTINE (*ibid.* 59) has described a new species of Hydnum from Pennsylvania.—CHARLES H. PECK (Bull. Torr. Bot. Club **31**:177–182. 1904) has published 16 new species of fleshy fungi.—A .W. EVANS (*ibid.* 183–226. *pls. 8–12.* 1904), in his fourth paper on the Hepaticae of Puerto Rico, has described *Cyclolejeunea* as a new genus containing four species.—H. CHRIST (Bull. Herb. Boiss. II. **4**:393–400. *pl. 1.* 1904) has described a new genus (*Loxsomopsis*) of Filicales (Loxsomaceae) from Costa Rica.—G. LINDAU (*ibid.* 401–418), in his third and closing paper on American Acanthaceae, has described *Juruasia* as a new genus.—K. GIESENHAGEN (Ber. Deutsch. Bot. Gesells. **22**:191–196. *pl. 13.* 1904) has described a new genus (*Sorica*) of Ascomycetes found attacking the sori of ferns.—F. HEYDRICH (*ibid.* 196–199) has described a new genus (*Stereophyllum*) of Corallinaceae.   AVEN NELSON (Bull. Torr. Bot. Club **31**: 239–247. 1904) has separated a new genus (*Chondrophylla*) from Gentiana and described new species in Eriogonum (2), Linum, Anogra, Pachylophus, Lavauxia, Gentiana, Hedeoma, Castilleja, and Symphoricarpos.—N. L. BRITTON (Torreya **4**: 93. 1904) has described a new Scirpus from Colorado.—FR. BUBÁK (Hedwigia **43**: 195–196. 1904) has described a new genus (*Lentodiopsis*) of Agaricaceae from Bohemia.—W. R. MAXON (Proc. U. S. Nat. Mus. **27**: 741–744. 1904) has described two new species of Polypodium from Jamaica.—E. ROSENSTOCK (Hedwigia **43**: 210–238. 1904) has begun a series of papers on the pteridophytes of southern Brazil.—P. HENNINGS (*idem* 242–273. *pl. 4*), in his second paper on Ule's collection of fungi from the Amazon region, has described *Hypoxylonopsis* (Dothideaceae), *Parmulariella* and *Uleopeltis* (Hysteriaceae), and *Rehmiomyces* (Bulgariaceae) as new genera.—F. VON HÖHNEL (*idem* 295–299) has described a new genus (*Atractina*) of Hyphomycetes.—W. A. MURRILL (Bull. Torr. Bot. Club **31**: 325–348. 1904), in his seventh paper on the Polyporaceae of North America, presents Hexagona (17 spp., 8 new), Grifola (6 spp., 1 new), *Romellia* (new genus), Coltricia (6 spp., 1 new), and *Coltriciella* (new genus)—O. F. COOK (*idem* 349–355), in a discussion of the nomenclature of the royal palms, has described a new genus (*Plectis*) from Guatemala.—G. E. OSTERHOUT (*idem* 357–358) has described new species of Arabis and Aulospermum from Colorado.—H. SYDOW (Ann. Mycol. **2**: 244. 1904) has described a new genus (*Rickiella*) of Ascomycetes.—F. VON HÖHNEL (*idem* 273–275) has described the new genera *Kordyanella* (Hymenomycetes) and *Debaryella* (Hypocreaceae).—THEO. HOLM (Am. Jour. Sci. IV. **18**: 12–22. 1904), in a report upon a collection of Canadian (British Columbia) Cyperaceae, has described a new Scirpus.—J. M. C.

# NEWS.

DURING THE RECENT MEETING of the British Association at Cambridge, th university conferred its doctorate of science on Professor ADOLF ENGLER and Sir W. T. THISELTON-DYER.

PROFESSOR JULIUS WIESNER and DR. LEOPOLD PORTHEIM, of Vienna, recently visited the University of Chicago on their way to the Yellowstone National Park; the former to study the light relations of plants, the latter the algae of the hot waters.

THE DAILY PAPERS announce the death of Dr. RUDOLPH A. PHILIPPI, the eminent German botanist, who has for more than half a century devoted his energies to the development of scientific work in Chile, especially in connection with the museum at Santiago.

M. A. CHRYSLER, of the University of Toronto, and later Fellow in the University of Chicago, has been appointed senior assistant in the Department of Botany of Harvard University. For the past summer he has been conducting ecological field-work for the Maryland Biological Survey.

THE PRELIMINARY program of the eighth international geographic congress, which convened in Washington, September 7-10, contained an announcement of a section for biogeography. In addition to papers by American plant geographers, announcement was made of papers by Professor FLAHAULT, of Montpellier, Dr. DRUDE, of Dresden, and M. CHRISTEN, of Bern.

AT THE SUMMER CONVOCATION (September 2) of the University of Chicago the degree of Ph.D. was conferred upon three candidates in botany. The names of the recipients and the subjects of the theses are as follows: W. J. G. LAND, "A morphological study of Thuja;" W. B. McCALLUM, "Regeneration and polarity in plants;" R. B. WYLIE, "The morphology of *Elodea canadensis.*"

THE INSTALLATION of Lanston monotype machines in the University Press has enabled the publishers to make notable improvements in the typography of the current volume of the BOTANICAL GAZETTE, to which we direct the attention of our subscribers. It will also be noticed that as the cost of composition has been thus reduced, the prices quoted for separates are 20 per cent. lower than formerly.

PROFESSOR N. L. BRITTON and DR. J. N. ROSE, having completed their monograph of the North American Crassulaceae, have undertaken a study of the Cactaceae. Dr. ROSE will spend considerable time in field work, especially in central and southern Mexico, where the Cacti are in inextricable confusion. There will be brought together first in New York and Washington large collec-

tions of living plants from which the descriptions will be drawn. Living material is desired from all parts of the southwest, and the National Museum will gladly furnish means for sending material to Washington.

DURING HIS VISIT to the United States, Professor HUGO DEVRIES has delivered courses of lectures at the University of California and at the University of Chicago. These lectures are to be published at once, and will bring to American readers a compact and clear exposition of the mutation theory and the experiments upon which it is based. At the University of Chicago, on September 2, Professor DEVRIES delivered the convocation address, his subject being "Evidence of evolution," and also received the honorary degree of LL.D. He is also to take part in the International Congress of Arts and Sciences at St. Louis, September 19–25.

THE PRIVATE HERBARIUM of Dr. JOHN K. SMALL consisting of 21,900 sheets, fully representing his collections in the southern United States, has lately been acquired by the Field Columbian Museum. The herbarium also contains several good series by other collectors. notably ROBERT BROWN's Australian plants; GARBER's Florida plants; HELLER's Virginia, North Carolina, and Pennsylvania plants; KEARNEY's Kentucky and Tennessee plants; LEWTON, BERG, and REYNOLD's Florida plants; ORCUTT's Lower California plants; PORTER's Pennsylvania plants; SMALL and HELLER's Pennsylvania, Tennessee, North Carolina, and Virginia plants; and WILKINSON's Mexican plants.

# Botanical Gazette

## OCTOBER, 1904

### THE RELATIONSHIPS OF SEXUAL ORGANS IN PLANTS.

#### CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXIII.

Bradley Moore Davis.

THIS paper will attempt a classification of the sexual organs of plants based upon certain evolutionary principles and involving phylogenetic relationships in so far as these are understood. With the classification is presented a terminology new in certain respects and restricting some older names to a more precise significance. The establishment of a terminology is of course a matter of usage. The present suggestions are not offered through the desire to create a new set of terms, but rather as a means of making plain the fundamental characters of the classification. But there are some features which if adopted would lead to much greater clearness of expression.

Almost all of the sexual organs of plants fall into one of three groups, quite distinct from one another, each marked by fundamental characters so well defined that one form cannot pass into the other except through great changes of structure and behavior. The only sexual organs whose positions do not seem to be clear in this classification are the complex multicellular structures of the lichens and the Laboulbeniaceae. The conditions in these interesting forms are very puzzling, and much more must be known of their cell and nuclear structure and developmental history before we can hope to place them in relation to other forms. The three great groups of sexual organs in plants are:

I. *Unicellular structures developing uninucleate gametes.*—These organs may be called collectively *gametocysts* or, when sexually dif-

ferentiated, the male becomes the *spermatocyst* and the female the *oocyst*. They are restricted to the thallophytes and are generally characteristic of the algae, but are not the only types of sexual organs found in this assemblage.

II. *Multicellular structures developing uninucleate gametes.*— These organs comprise the antheridia and archegonia of the bryophytes and pteridophytes, which have probably been derived from a multicellular structure whose gametes were sexually undifferentiated (isogamous), which structure would be included under the more general term *gametangium*. In a harmonious terminology based upon the gametangium the male organ might be called a *spermatangium* and the female an *oangium*. Gametangia are represented among the thallophytes by the so-called plurilocular sporangia. Spermatangia (antheridia) are found in the Charales and Dictyota.

III. *Multinucleate sexual cells or coenogametes.*—These remarkable sexual organs, named by the author "coenogametes" (DAVIS '00, p. 307), are most typically illustrated in the Mucorales and Gymnoascales, but are also found in a somewhat modified form in the Saprolegniales, Peronosporales, and certain Ascomycetes. Coenogametes are morphologically either gametocysts that have become changed directly into gametes, or they are restricted portions of such cells.

These types of sexual organs will be considered in order, with a brief summarized list at the end of the paper.

### I.  GAMETOCYSTS, SPERMATOCYSTS, AND OOCYSTS.

The terminology which we shall use for the simplest sexual organs of plants (*unicellular structures developing uninucleate gametes*) is based upon suggestions of VUILLEMIN ('02) presented for the purpose of clearly separating this group from the multicellular reproductive organs characteristic of plants above the thallophytes. The unicellular sexual organ is well known to have had its origin from a reproductive cell which produced asexual spores, and such may be called a *sporocyst* consistently with the other terms. The list of unicellular reproductive organs leading to the high sexual conditions of the heterogamous algae, such as Volvox, Oedogonium, Vaucheria, the Cyclosporeae, and the Rhodophyceae, is then as follows:

Sporocyst, a unicellular structure producing asexual spores.
Zoosporocyst, a unicellular structure producing zoospores.
Gametocyst, a unicellular structure producing uninucleate gametes.
Spermatocyst, a unicellular structure producing sperms.
Oocyst, a unicellular structure producing eggs.

The terms sporangium, gametangium, antheridium, and oogonium, which have been applied to the above structures and to others as well, have been reserved for more precise usage, as will appear later in the paper.

It should be noted especially that this list includes the sexual organs of almost all of the groups of algae, forms which illustrate the usual course of sexual evolution. The principal stages and steps in the origin and evolution of sex are fairly well understood. The writer has recently described them (DAVIS '01, '03a) and will not take up the matter further than to emphasize some facts which have important bearings on the subject of this paper.

The gametocyst came into existence with the origin of sex, and was derived from a zoosporocyst whose zoospores became physiologically sexual. Sex has probably arisen a great many times in the plant kingdom, since it is fundamentally only a physiological condition, but so far as we know the origin has always been the same, namely through the conjugation of motile cells.

With the gametocyst established, there is sure to follow a tendency to differentiate the structure according as the sexual cells assume more and more the characters of sperms and eggs. The differentiation of sex is well known to be one of the results of plant evolution which has appeared in a number of divergent lines of ascent entirely independently of one another. The eggs and sperms of widely separated phyla in the algae, as for example those ending in Volvox, Vaucheria, Coleochaete, and Fucus, can only be related through their origin from the undifferentiated gametes or zoospores of a distant ancestry. So the mother-cells, oocysts, and spermatocysts of these sexual elements are related in the divergent lines among the algae only through an ancestry from the undifferentiated gametocyst or its progenitor the sporocyst.

There are several groups of algae which offer interesting peculiarities of structure that demand special explanations. In the filamentous Conjugales we have the union of gametes while still contained

within the cellulose walls of the gametocysts. This is far from a simple sexual condition, and it is a great mistake to present these types as illustrations of primitive sexuality. It is possible that the Conjugales have come by way of the unicellular forms related to the Volvocaceae, whose cells adopting quiescent habits gave rise to the desmids, through which the filamentous Zygnemaceae and Mesocarpaceae may have been derived. In many of the desmids the gametes escape from the gametocysts to fuse as naked masses of protoplasm. The retention in the Zygnemaceae and Mesocarpaceae of these gamete protoplasts within the gametocyst, and the consequent fusion of sexual cells surrounded by a cellulose wall is a peculiarity identical in this respect with the fusion of coenogametes in the Mucorales, Peronosporales, and lower Ascomycetes, and is evidence of a highly specialized sexual condition.

In the Rhodophyceae the spermatocysts have the peculiarity of producing each a single non-motile sperm, and the oocyst (carpogonium) develops a long filamentous receptive outgrowth, the trichogyne, surrounded by the cell wall, with which the sperm fuses. There is here, therefore, as in the filamentous Conjugales described above, the fusion of gamete protoplasts while still surrounded by their respective cell walls. Eliminating this peculiarity and the production of non-motile sperms, the sexual organs of the red algae appear to be similar to those of Coleochaete. There are some possibilities, however, which may complicate the problem of the classification of the sexual organs of the Rhodophyceae, and may relate it to the puzzling conditions in the Laboulbeniaceae and lichens. I refer to the presence of a trichogyne nucleus in Batrachospermum reported by myself, and the binucleate sperms described by Schmidle ('99). We may find here and in other red algae peculiarities with direct relationships to the two fungal groups mentioned above.

The Charales present extraordinary conditions. The female organ is apparently an oocyst, surrounded, however, by a complex envelope of investing filaments; while the male organ is multicellular and consequently is not a spermatocyst, but falls within the second group of sexual organs, although it can hardly be supposed to have genetic relation to these. The spermatangium (antheridium) of the Charales is certainly one of the puzzles of plant morphology.

The male organs of some other algae, as Oedogonium, are groups of closely related cells which constitute a simple tissue, and similar conditions are also found in the Rhodophyceae, but all of these structures are really clusters of spermatocysts, and can scarcely be considered differentiated organs of the plants, even though they sometimes have very definite form. Nevertheless, the structures frequently are so constant as to have taxonomic value, and consequently probably always will be called antheridia in the works which deal with such matters.

The sexual organs of Dictyota present conditions that make their classification difficult. The cells producing male elements become divided (see figures of WILLIAMS '04) into a very large number of compartments, each of which develops a solitary sperm. This structure seems to be the same as that of the so-called plurilocular sporangia of the Phaeophyceae, in which case the male organs cannot be called sporocysts, but are true spermatangia (antheridia). The eggs, however, are formed singly in the mother-cells, which are therefore oocysts. The significance of these mixed characters in the group is not clear. Either the spermatangia (antheridia) are derived from spermatocysts that have adopted the peculiar methods of extensive cell division characterizing plurilocular sporangia, or the oocysts stand as the final stage in a remarkable reduction and final suppression of such activities in an ancestral multicellular female organ (oangium).

The desirability of some system and uniformity in the nomenclature of a group of reproductive organs which are clearly homologous (as are the sporocyst, gametocyst, spermatocyst, and oocyst) lies of course in the greater clearness and simplicity of the conception and expression of these relationships. The adoption of a new terminology for these structures will depend upon how strongly botanists may feel the need of these changes. Such old names as sporangium, gametangium, antheridium, oogonium, and ascogonium would be restricted to a narrower application, but, as we shall presently explain, they need not be entirely discarded.

It will be asked what are the particular advantages of the set of names proposed (sporocyst, gametocyst, spermatocyst, and oocyst) over older terms, and why have not the latter been retained and new

names proposed for the other great class of sexual organs, the multi-
cellular structures?   The principal reason for the present suggestion
is the desirability of naming unicellular structures in a manner indica-
tive of their morphology.   A better set of names would have been
sporocyte, gametocyte, spermatocyte, and oocyte, but the last two
terms have a special and precise significance in zoology.   There is
no evidence of exact correspondence between the events of spermato-
genesis and oogenesis in animals and plants, but on the contrary
many reasons for believing that the processes have not only had an
independent origin, but have developed along quite different lines.
This subject cannot be treated at this time, but for these reasons we
have avoided the term spermatocyte and oocyte, and instead have
made use of VUILLEMIN's suggest ons.

### II.   GAMETANGIA, SPERMATANGIA, AND OANGIA.

The second group of sexual organs comprises *multicellular struc-*
*tures which develop uninucleate gametes*.   The fully differentiated
organs are best illustrated by the antheridia and archegonia of the
bryophytes and pteridophytes, but these heterogamous conditions
must have arisen from a simpler type of gametangium, and this must
be sought among the thallophytes.   The writer (DAVIS '03) has
recently suggested their origin from a type of structure something
like that of the plurilocular sporangium of the Phaeophyceae and
the multicellular fruiting branches of such green algae as Schizomeris,
*Stigeoclonium tenue irregulare,* and the conditions sometimes found
in Draparnaldia and Chaetophora.

It will be difficult to displace such firmly established names as
antheridium and archegonium, but a terminology may be constructed
with sporangium and gametangium as a basis which is as consistent
and harmonious as that proposed for the first group of organs.   It
would be as follows:

Sporangium, a multicellular organ producing asexual spores.
Zoosporangium, a multicellular organ producing zoospores.
Gametangium, a multicellular organ producing uninucleate gametes.
Spermatangium (antheridium), a multicellular organ producing sperms.
Oangium (archegonium), a multicellular organ producing eggs (VUILLEMIN
    '02).

The origin of the sexual organs of the bryophytes and pterido-
phytes is necessarily a matter of speculation, but the relation that
they bear to one another and the type of structure which they repre-
sent are much more clearly understood than formerly.   These game-
tangia are essentially cellular capsules composed of an outer layer
of sterile cells which encloses a central mass of gametogenous tissue.
The development of the antheridium and archegonium generally
starts from a superficial cell, which by various divisions differentiates
a single terminal cell or a group of terminal cells that become the
growing points of the structure, building it up from above.   Thus the
antheridium and archegonium are from the beginning and at all
times tissues of a definite form whose cooperating cells establish the
organ.   They are not structures of the same class as certain assem-
blages of independent gametocysts whose cells are massed into definite
form, as for example many so-called antheridia of the red algae.

It seems to be perfectly clear now that the central region of cells
within the capsule wall of both antheridium and archegonium are
phylogenetically gametogenous tissues and are homologous; or,
expressed concretely, that the canal cells of the archegonium are
reduced and degenerate gamete mother-cells which together with the
fertile egg cell are homologous with the sperm mother-cells.   This
view, which has been held tentatively by many botanists for a long
time, is supported especially by observations by Hy and Treub,
and the recent studies of Holferty and Lyon.   Goebel ('02) in
an important paper has discussed the homologies of the sexual organs
in bryophytes and pteridophytes, recognizing that the suppression of
cell division and a process of sterilization were largely responsible for
the peculiarities of the female.   He also clearly showed the difficulties
that throw so much doubt on Götz's theory of a relationship between
the archegonium and oogonium of the Charales.

Hy ('84, p. 121) noted that various species of mosses present occa-
sionally the transformation of archegonia into antheridia, a phenome-
non apparently frequent in *Atrichum undulatum*.   Treub's ('86,
pp. 107–108) observations on *Lycopodium Phlegmaria* are of the
greatest significance.   He found that the canal cells may contain two
nuclei, and he figures an archegonium in which a canal cell is divided
longitudinally so that the axial row is double at that point.   A dia-

gram which the author introduced to illustrate a theoretical stage in the evolution of the archegonium (DAVIS '03 *c*, p. 491, *fig. 21, c*) unwittingly almost duplicated this figure (TREUB '86, *pl. 21, fig. 9*), to which his attention was called after the publication of this paper. TREUB also noted the transformation of archegonia into antheridia and archegonia whose tips remained closed and became abnormally swollen. Recently HOLFERTY ('04) has determined for Mnium that the series of canal cells is sometimes a double row for a greater or less distance instead of the single line usually present, that the egg and ventral canal cell are usually of nearly equal size, and that occasionally organs are found with mixed antheridial and archegonial characters, as when portions of an evident axial row break up into sperm mother-cells. A number of observers have reported abnormalities among the mosses, such as archegonia with two eggs, with two venters, or with enlargements of the neck regions. These conditions all appear to justify entirely the conclusions of the previous paragraph.

Especially interesting are some illustrations of unusual conditions in the pteridophytes brought together by Miss LYON ('04). There are the two canal cells that normally lie side by side above the ventral canal cell of Equisetum, a condition also found in Isoetes. Two eggs are occasionally present in the archegonium of *Selaginella apus*, and a pair of eggs, one above the other with two canal cells between, have been observed in *Adiantum cuneatum*. The most remarkable conditions, however, are those found in *Lycopodium complanatum*, whose deeply imbedded archegonia have sometimes as many as fourteen to sixteen cells in an axial row, over half of which, and sometimes the egg cell itself, are binucleate. Thus the observations of TREUB ('86) on *Lycopodium Phlegmaria* are substantiated, and it is likely that others of the Lycopodiaceae have archegonia of a generalized type, with large amounts of potential gametogenous tissue. They present conditions that may be expected in any primitive group of bryophytes or pteridophytes. For male organs Miss LYON contributes a new fact in finding submerged antheridia in *Lycopodium annotinum*.

The evolutionary tendencies of antheridia and archegonia, from their most generalized conditions among the bryophytes, are evidently in the direction of numerical reduction of the number of gamete

mother-cells and the amount of sterile tissue developed. These
tendencies are plainly shown in comparisons of the sexual organs of
the pteridophytes with those of the bryophytes. The antheridia of
the former group are all very much smaller than those of the latter;
the wall of the capsule contains relatively few cells and the amount
of spermatogenous tissue is very much reduced. Thus where thou-
sands of sperms are developed in each antheridium of the bryophytes,
there are less than a hundred formed in most of the pteridophytes, and
sometimes very few (four in Isoetes). The archegonia of the pteri-
dophytes have a smaller number of cells than those of the bryophytes.
The neck region is much shortened and the number of canal cells
becomes reduced from a large number in the bryophytes to two or
three in some pteridophytes. Physiologically this reduction in the
number of gametes, together with the greater specialization of egg
and sperm, follows a history generally parallel with that in the thallo-
phytes, and is what should be expected in any series of plants subject
to the conditions that lead to the high levels of sexual evolution.

The history of the antheridium and archegonium in the reduced
gametophytes of seed-bearing plants is not well understood, but
this is not the time to discuss such difficult and highly special problems
as the homologies of the stalk and body cell of the pollen grain or the
egg apparatus and antipodals of the embryo sac. It is certain from
the transitional conditions presented in the gymnosperms that the
sperm and egg nuclei of the spermatophytes are homologous with the
same gamete nuclei of the pteridophytes, and that they stand for
antheridia and archegonia which have lost most and in some cases all
of the sterile tissue characteristic of these organs as found in the
bryophytes and pteridophytes.

With respect to the origin of the antheridium and archegonium,
the investigations of HOLFERTY are strongly in support of the hypothe-
sis previously suggested by the author (DAVIS '03 c). This hypothesis
may be briefly summarized as follows: Since the antheridium and
archegonium are multicellular structures from the beginning, and are
morphological units developing from well-defined growing points,
they cannot have been derived directly from the unicellular sexual
organs (gametocysts) generally present in the thallophytes. They
must have arisen from a multicellular structure (gametangium),

which was probably at the level of isogamy in its sexual evolution, because the gametogenous tissues in the antheridium and archegonium are essentially similar in structure, as is also true of the sterile tissue forming the surrounding capsule. The only multicellular reproductive organs of the thallophytes which offer any possible points of relation seem to be the so-called plurilocular sporangia or gametang'a of the Phaeosporeae, and similar structures in certain green algae, Schizomeris, *Stigeoclonium tenue irregulare,* and conditions occasionally found in Draparnaldia and Chaetophora. Such multicellular reproductive organs of course must be regarded only as representatives of a certain type of structure (sporangium or gametangium), and not as direct ancestors of the sexual organs of bryophytes and pteridophytes. I have never associated the archegonium closely with any individual form as Miss Lyon ('04, p. 281) might lead one to suppose.

These sporangia and gametangia of the brown and green algae have the peculiarity that the original cells divide up into a great number of very small cells (loculi), each of which often develops but a single zoospore or gamete. It is probable that the extensive cell division by which each zoospore or gamete is often given a separate compartment in the general structure is responsible for the origin of a multicellular reproductive organ (sporang'um or gametangium) from some type of unicellular structure (sporocyst or gametocyst). These sporangia and gametangia of the brown and green algae are known to be modified branches, generally somewhat smaller than vegetative branches. Should such gametangia be placed under environmental conditions demanding protective coverings (as by a change from water to a land habitat), the first expression would be the sterilization of the outer layer of cells to form a protective capsule around the interior gametogenous tissue. Such an advance would give the essential structure of an antheridium and an archegonium, and further specialization need be only along the well-known lines of sexual differentiation, by which one form of gametes would become somewhat modified as small sperms, and the other form, by loss of motility and through numerical reduction and consequent conservation of material for a few gametes, would become large eggs. These matters have been discussed in full in the author's paper on "The origin of the arche-

gonium" (DAVIS '03 c) and the reader must be referred to that for a detailed treatment of the subject.

Miss LYON ('04) has discussed the interesting problem of the relation of the sunken gametangia, characteristic of certain pteridophytes (especially Lycopodium) and such liverworts as Anthoceros and Aneura, to the stalked archegonium and to my theory associating these structures with plurilocular sporangia. She is inclined to derive the sunken structure from an indeterminate region of gametogenous cells which later might develop into an emergence with the general characters of a gametangium (plurilocular sporangium). This view carries the origin of the archegonium still further back, and allows the organ to develop through an emergent gametangium into the stalked structure, or to remain partially or wholly imbedded in the tissues of the gametophyte. In the first group the archegonia would become definite gametangia, comparable to plurilocular sporangia; while in the second they would remain as less defined or indeterminate regions of gametogenous tissue. The chief difficulties in this view, in the author's opinion, lie in the remarkable unity of structure displayed by the archegonium, in the presence of a single terminal opening, and the situation of the egg at the bottom of an axial row of gametogenous cells, which conditions imply an origin from some definite type of gametang'um whose fertile tissue was limited to a central region. The rarity among the known thallophytes of indeterminate regions of gametogenous tissues present further important difficulties in Miss LYON's theory.

Miss LYON ('04, p. 289), however, is inclined to pass lightly over the latter difficulties, believing that transitory conditions may "be readily found among the algae." She discusses several types and presents a diagram of Ulva indicating a gametogenous tissue of considerable thickness at the period of reproduction. This is a very deceptive diagram, for not only are there no walls formed between the successive segments of protoplasm in the mother-cells, but the latter are remarkably well-defined sporocysts, each independent of its neighbors. The membrane of Ulva is very far from constituting a thallus several layers of cells thick, or even a differentiated tissue. In Phyllitis there appears a successive segmentation of the protoplasm within the mother-cells with the formation of walls by which the

zoospores or gametes are finally developed, each in its own compartment, and this fact makes the group of cells derived from each mother-cell a sporangium or gametangium. The groups are quite independent of one another and there is little hint of a tissue. Essentially the same conditions are found in Punctaria. Porphyra is probably very similar to Ulva in its methods of spore-formation, whatever may be the significance of the so-called antherozoids and carpospores. I am impressed with the exceeding rarity in the thallophytes, and indeed in all plants, of indeterminate regions of gametogenous tissue, and I know of no form that illustrates clearly Miss Lyon's conception of primitive conditions such as she has tried to illustrate by her diagrams of Ulva.

Miss Lyon might have made her case appear stronger on first glance by citing Schizomeris and Pylaiella as illustrations of "indeterminate masses of reproductive cells." In these two types the sporocyst and sporangium or gametangium come so close together that the general morphology of the respective fruiting filaments is almost identical. The distinctions, however, lie in the presence of very numerous cell walls which are never found in sporocysts, and which give the compartment structure to the sporangium and gametangium.

The development of cell walls following the segmentation of protoplasm during sporogenesis may seem a very insignificant factor on which to base a broad classification, but I think that close examination will prove it to be of fundamental importance, because the introduction of these walls transforms a reproductive cell into a tissue, however simple the arrangement may be. I doubt if it is possible to derive a clearly defined structure from the mere association of a group of sporocysts or gametocysts, without the cell divisions indicated above which immediately change the groups of reproductive cells into sporangia or gametangia. When a number of closely associated reproductive mother-cells divide in this manner, the tissue may become quite extensive, and if these cells make up a well-defined structure, as perhaps a filament or some emergent region, there is at once developed an organ. There are abundant illustrations of these simple conditions, in various stages of relative complexity, in the Phaeosporeae; for example the Ectocarpaceae present a wide range from the generalized fruiting filaments of Pylaiella to the specialized sporangia and gametangia (plurilocular sporangia) of Ectocarpus.

In this distinction of protoplasmic behavior during sporogenesis and gametogenesis (*i. e.*, the formation of cell walls during the segmentation of the protoplasm) lie the fundamental peculiarities of the sporangium and gametangium.   And in this distinction are based my views of the homologies and origin of these structures.   Associated with the peculiarity is the fact that sporangia and gametangia are almost universally superficial, and perhaps always have their origin from superficial cells.   There may be exceptions to this general rule, as the antheridia of Anthoceros and some sunken sexual organs of the Lycopodineae, but these have not been sufficiently studied to justify conclusions.   Thus, EMMA LAMPA ('03) has obtained Anthoceros plants bearing antheridia of superficial origin, and regards these as representing primitive conditions, and one cannot guess what investigations among the pteridophytes may bring forth.   The reasons for the superficial position of reproductive organs are probably at bottom physiological, although of course one may readily advance teleological explanations.

I do not find the same difficulty as Miss LYON in deriving the generalized and sunken sexual organs of some pteridophytes, notably the Lycopodineae, from superficial structures.   Of course one does not relate them to extreme emergent types, such as are found in the Jungermanniales and Marchantiales.   But a simple type of archegonium, sessile upon the gametophyte, might incorporate adjacent cells into its structure, especially if these are so generalized in character as to have reproductive potentialities, and thus become a more or less sunken structure.   The emergence of an archegonium depends chiefly on the pushing out of a superficial cell, from which, so far as we know, the neck region is derived as from a growing point.   And the egg in many sunken archegonia unquestionably takes its position because adjacent cells develop an uplifted portion of the gametophyte around it.   Gametangia which are deeply sunken in the gametophyte, as in Lycopodium (and few have been reported), are perhaps as extreme in the direction of suppression as are the gametangia of mosses and most liverworts in the direction of emergence.   These submerged sexual organs present difficulties that demand special investigation as to their origin.   Thus, there may be an evolution of the sessile gametangium in both directions, on the one hand

leading to uplifted stalked structures and on the other resulting in a submerged condition. We know at present too little of the comparative structure and development of the archegonium and antheridium, to define safely the evolutionary tendencies throughout the various groups of the pteridophytes.

### III. COENOGAMETES.

Coenogametes (DAVIS '00, p. 307) are *multinucleate sexual cells* and are morphologically either gametocysts that have become changed directly into gametes or they are restricted portions of such cells. Recent investigations have established their presence in various Phycomycetes and Ascomycetes, and it is probable that future studies will show them to be a type of sexual organ common in these regions of the plant kingdom. We do not know enough to justify speculation as to the exact relationships of these structures, but it is not likely that they are all closely related to one another, and it is very probable that various types of coenogametes may have arisen independently.

Coenogametes fall into two classes: (1) those in which all of the protoplasm of the parent cell is retained in the gamete; and (2) those in which only a portion of the protoplasm is thus utilized, the remainder being devoted to other functions than that of reproduction. It is not perfectly clear as yet whether the evolutionary tendencies are from the first group towards the second or *vice versa*, or perhaps irregularly both ways. But from our knowledge of the lines of sexual evolution in the other two groups of sexual organs (gametocysts and gametangia), the author believes the general advance to be from the simpler first class of coenogametes to the more complicated second class.

Coenogametes of the first class are best illustrated by the sexual organs of the Mucorales and the Gymnoascales. The latter group has been recently studied by Miss DALE ('03), who finds that the earliest stage of the gamete is a uninucleate cell which becomes multinucleate as it increases in size. After the union of these coenogametes the ascogenous hyphae develop from a coiled prolongation that grows out from the fusion cell. We do not know the history of the nuclei in the fusing gametes of the molds or in Gymnoascus, but there is every reason to expect that most of them unite in pairs, as is

the case under similar conditions in *Albugo Bliti* and Pyronema.   It
is probable that the conditions in Gymnoascus will be found to be
generally present in what are usually called the lower groups of the
Ascomycetes.   It looks very much as though such genera as Eremas-
cus, Eurotium, Ceratostoma, Sordaria, and Ascobolus will be found
to present sexual organs essentially similar to those of Gymnoascus.
Their general agreement with the sexual processes of the Mucorales
may have great significance in connection with the origin of the
coenogamete and possible relation of the Mucorales and Ascomycetes
to one another or to a common algal ancestry.

Coenogametes of the second class are much better understood with
respect to the details of protoplasmic structure and behavior than those
of the first class.   The development of the sexual organs and processes
of fertilization are perhaps as well known in Albugo (STEVENS '99,
'01) and Pyronema (HARPER '00) as for any plant types.   In *Albugo
Bliti* and *A. Portulacae* the ooplasm contains numerous nuclei, and
an equally large number is introduced into the egg from the male
coenogamete, these sexual nuclei then fusing in pairs.   Other species
of Albugo (*e. g., A. Tragopogonis*) show a lessening number of func-
tional and potential gamete nuclei in the egg, until forms are reached
in *A. candida* and *A. Lepigoni* (RUHLAND '03) whose eggs are nor-
mally uninucleate.   This series in the genus Albugo, so well described
by STEVENS ('01), is very interesting and we shall refer to it again.
All other genera of the Peronosporales have, so far as is known,
uninucleate eggs (Pythium, Peronospora, Sclerospora, and Plasmo-
para).   In Pyronema there is developed a conjugating tube that takes
out of the female coenogamete many of its nuclei.   But a very large
number are left in the structure, and these fuse in pairs with numer-
ous male nuclei that enter the female cell by way of the conjugating
tube.   The female coenogamete of Monascus, according to BARKER
('03), cuts off a sterile cell and thus disposes of some of its protoplasm.
The recent discussion of IKENO ('03) as to the systematic position of
BARKER's form deals with the life history after fertilization.   There
is no criticism of BARKER's account of the structure of the sexual
organs.   Although not positively established, there are good reasons
for believing that the numerous gamete nuclei of Monascus fuse in
pairs as in *Albugo Bliti*, *A. Portulacae*, and Pyronema.

The Perisporiaceae, Lichenes, and Laboulbeniaceae among the Ascomycetes present sexual organs of a highly differentiated character. These are very much specialized groups whose morphology and life histories indicate a degree of development and differentiation far above most of the simpler forms that we have just discussed (Gymnoascus, Monascus, Pyronema). The gametes of Sphaerotheca (HARPER '95, '96) are uninucleate, and it becomes an interesting problem whether or not this form stands at the end of a series representing nuclear reduction from a coenogamete, such a series as is illustrated by the species of Albugo. The recent studies of BAUR ('98, '01) and DARBISHIRE ('00) on the lichens have clearly established the sexuality of these forms and the significance of the ascogenous hyphae. But we do not sufficiently know the nuclear conditions to justify any extended speculations on the homologies of the cells in the archicarp and trichogyne of the female sexual organ. And similarly the sexual organs of the Laboulbeniaceae (THAXTER '96) present most interesting and puzzling complications of cell structure that cannot be explained until we know the detailed history of the nuclei in the processes of development and fertilization.

In a discussion of the origin and evolution of coenogametes much depends upon the relation of the structures in the first and second class. Which is the more primitive type? Some botanists will claim that conditions of the first class (Mucorales and simpler Ascomycetes) illustrate degeneration from higher sexual forms. The author is of an opposite opinion, believing that the coenogametes of the first class illustrate closely the conditions of very simple and the most primitive types of coenogametes. This view has been discussed in a previous paper (DAVIS '03 b, pp. 233–327, and 331–339), but may be summarized briefly here.

The coenogametes of the first class are morphologically gametocysts which have given up the function of forming numerous gametes (represented by the many nuclei), but obeying chemotactic influences of a sexual character fuse with one another as coenocytic units. They would represent a relatively low level of sexuality (isogamy), and their progenitors would be looked for among groups whose gametocysts discharged motile gametes that fused in pairs, as is illustrated among the isogamous Siphonales. An ancestry of this

character under certain conditions, as through a change from aquatic to aerial habits, might give up the habit of developing motile sexual elements, which would be represented, however, by the numerous gamete nuclei fusing-in pairs in the cytoplasmic union of the parent coenogametes. We have excellent illustrations of the sacrifice of motile spore-forming habits in the conidia of Peronospora and some species of Pythium, which germinate by a tube instead of developing zoospores. These conidia are morphologically sporocysts which have become coenocytic units, and coenogametes are gametocysts which have become coenocytic units. It must not be supposed that coenogametes are all related to one another. They might readily arise, according to our theory, from various types and at different times, thus making possible a number of developmental lines.

The coenogametes of the second class are restricted portions of cells, which like those of the first class are morphologically gametocysts. Indeed in many cases the mother-cell is essentially a unit, even though only a part of the protoplasm is actually the sexual element, because the remainder has some special relations or functions in connection with the sexual processes. Thus the periplasm of the Peronosporales and the conjugating tube of Pyronema hold such intimate relations to the sexual portion of the protoplasm that the entire gametocyst is really a coenocytic unit, and might be called the coenogamete instead of the restricted portion that is actually fertilized. From the conditions in the genus Albugo it would seem that some coenogametes of the second class follow the general law of sexual evolution, reducing the number of functional gamete nuclei until the eggs are uninucleate. The series from *Albugo Bliti* and *A. Portulacae* through *A. Tragopogonis* to *A. candida* and *A. Lepigoni* is a most interesting one, and the author (DAVIS '03 *b*, p. 323, 324) has already expressed his agreement with STEVENS and RUHLAND that the drift of development in the genus is plainly in the above order, from the multinucleate to the uninucleate egg. We may hope with increasing studies on the sexual organs of Ascomycetes to discover evolutionary lines in this group, but our knowledge is entirely insufficient at present to justify conclusions. Thus, uninucleate gametes like those of Sphaerotheca may represent the last stage in a process of nuclear reduction. And along a very different line such

structures as conjugation tubes (Pyronema), accompanying sterile cells (Monascus), or an investing cellular envelope (Araiospora) might give rise to more conspicuous accessory structures.

It need not be supposed that coenogametes of the second class are all derived from those of the first class, and in some regions there are good reasons for believing that this has not been the case, especially since the processes of oogenesis in Vaucheria (DAVIS '04) conform in the most essential features with those of the Peronosporales and Saprolegniales. These three groups agree in the fundamental fact that extensive nuclear degeneration takes place in the gametocysts previous to the formation of the sexual cells. In Vaucheria all but one of the nuclei become disorganized. In Saprolegnia a number survive in relation to several coenocentra that determine the position of the eggs which are occasionally bi- and trinucleate. In the Peronosporales the surviving nuclei lie in the ooplasm, and when only one is selected it is because of close proximity to the large coenocentrum. These conditions in the Peronosporales and Saprolegniales are so similar to one another and to Vaucheria in various particulars that there are evident relationships, but whether these are direct or more general by way of a common ancestry among the lower Siphonales is a problem that perhaps may be better handled when we know more clearly the processes of oogenesis in such forms as Sphaeroplea, Monoblepharis, and some other types. Their processes of oogenesis are likely to conform to the type in Vaucheria.

Whatever may have been the origins of the several types of coenogametes representing the second class, problems which are very difficult and perhaps impossible to solve with the fragmentary evidence left to us, we can at least attempt to judge the probable direction of their development, and possibly establish some system or law of their sexual evolution. As stated before, some botanists will hold that even the simplest forms of coenogametes (Mucorales and Gymnoascales) have been derived from heterogamous algae by processes of simplification or degeneration. The author cannot take this attitude, believing as he does that the simplest coenogametes have had their origin from isogamous algae, that they may tend to pass into higher conditions leading to those of heterogamy, and that very much the same factors are at work to differentiate the sexual elements in this region of the plant kingdom as among the algae.

The old group of the Oomycetes has been a favorite starting point for evolutionary lines in the Ascomycetes and Mucorales. DeBary pointed out the resemblances between the Ascomycetes and members of the Peronosporales, and since his time a number of writers have traced lines of relationship with greater or less detail. The most recent expression, that of Barker ('03), considers Albugo as presenting sexual organs sufficiently primitive to be like the progenitors of the Ascomycetes. The less complicated sexual organs of Gymnoascus, Eremascus, etc., and the similar conditions in the Mucorales have very generally been regarded as derived from higher conditions (as in Albugo) by a process of simplification or degeneration, whereby sexually different gametes become essentially similar.

The two regions of the algae most discussed in attempts to establish points of origin of the higher Phycomycetes and Ascomycetes have been Vaucheria and the Rhodophyceae. The resemblances of Vaucheria to the Peronosporales and Saprolegniales are very striking, the more so since the recent studies in oogenesis have brought all groups into close sympathy. The author believes that that there are relationships here, although probably they are not direct. But when the Mucorales are annexed on the theory that the highly differentiated sexual organs of heterogamous groups may become generalized to those of the molds, then difficulties appear which seem at present insurmountable. There is no morphological evidence of such a line of development, and the process as a physiological event would be quite unparalleled and contrary to all known principles of sexual evolution. And similarly Barker's view that *Albugo Bliti* presents sexual conditions simple enough for the most primitive ascomycete does not seem to the author justified by its cell and nuclear activities (Davis '03 *b*, pp. 344, 345).

The remarkable resemblances between the Laboulbeniaceae and the Rhodophyceae have been noted by Thaxter ('96), who has suggested that the Ascomycetes may have arisen from this point in the plant kingdom. The similarity of the Laboulbeniaceae to the red algae is certainly very striking, and there are no more interesting problems in this region of plant morphology than those involving careful comparisons of the sexual processes and the development of the cystocarp and ascocarp in these two groups. There are indica-

tions among the red algae in the trichogyne nucleus of Batrachospermum and its binucleate sperms (SCHMIDLE '99) of conditions which if found more generally may assist to a clearer understanding of these remarkable fungal groups and materially support THAXTER's view.

It is very difficult to conceive a relationship between the sexual organs of the simpler Ascomycetes (Gymnoascales, etc.) and those of the lichens and Laboulbeniaceae. One can scarcely conceive of a process of simplification by which the former could have come from the latter. On the other hand, the general principles of sexual evolution operating upon the simple sexual organs of the lower Ascomycetes would be more likely to result in the conditions illustrated by Monascus, Pyronema, and Sphaerotheca than those of the lichens and Laboulbeniaceae. Such an evolution would also be in sympathy with the general ascending complexity of vegetative thallus and ascocarps in the forms under consideration. This view would place the progenitors of the simpler Ascomycetes in a region much lower than the Rhodophyceae, and perhaps relate them to certain Phycomycetes. There is of course the possibility of the Ascomycetes being polyphyletic, removing the Laboulbeniaceae from the general assemblage, which might dispose of these difficulties, but we must know much more about the comparative development of the ascocarps in the groups before such a view can be considered well-founded.

The author cannot agree with any view that fixes the origin of the Mucorales and Ascomycetes from conditions illustrated by any known living form. The problems of relationship involve so many considerations, those of taxonomy as well as evolutionary tendencies in sex, that arrangements of living types in series seems futile. He believes that the most hopeful line of speculation will be founded on the close study of the principles of sexual evolution and a comparison of forms in this light, with such checks as may be furnished by the comparative morphology of all phases in the life history of the types. And these principles indicate to the author much simpler primitive sexual organs for the Ascomycetes and Mucorales than have been supposed, and with their origin below the Peronosporales (Oomycetes), and perhaps finally, for the Mucorales at least, from the isogamous Siphonales (DAVIS '03, p. 335).

We cannot at this stage in the progress of investigations give a

precise statement of the evolutionary tendencies of coenogametes, but certain factors may be considered, of which the principal ones seem to be cooperative in both the Phycomycetes and Ascomycetes. Assuming that coenogametes may have arisen at various times independently of one another, and from an ancestry at approximately the level of isogamy or slightly above it, their evolution might proceed along three or more divergent lines. They all agree in having very numerous potential gamete nuclei, and there is strong evidence from the processes of gametogenesis in Saprolegnia, the Peronosporales, Pyronema, and Vaucheria that these are under conditions which demand extensive nuclear degeneration. Consequently the evolutionary tendencies are largely concerned with the disposition of superfluous nuclei and seem to present the following possibilities.

I. General nuclear degeneration may result in the survival of a few gamete nuclei in relation to coenocentra and the development of a limited number of eggs, as in the Saprolegniales.

II. Superfluous nuclei with some cytoplasm may be differentiated as a periplasm, with functions to perform in laying down portions of the spore wall, which conditions accompanied by numerical reduction of the nuclei in the ooplasm give the general tendencies in the Peronosporales. There is apparently presented in Araiospora (KING '03) a modification of the habits in the Peronosporales, since the periplasm in this form develops a cellular envelope around the spore.

III. In the Ascomycetes we have a much wider range of conditions, with proportionally much less knowledge of the forms, so that the working out of evolutionary lines becomes very speculative. However, superfluous protoplasm with nuclei is used here to form accessory structures, such as the conjugation tube of Pyronema and the sterile cell of Monascus. There is probably also numerical nuclear reduction, which would culminate in uninucleate gametes, as in Sphaerotheca. The multicellular trichogynes and archicarps of the lichens and the Laboulbeniaceae present some very difficult morphological problems, with possible relations, however, to conditions in the Rhodophyceae, especially should further study in the latter group establish the presence of multinucleate sexual organs.

The suggestions of the paragraph above must of course stand the test of extensive investigations on many more forms and with refer-

ence to points of general morphology as well as those that concern the sexual organs alone. The former would have been treated by the author had they appeared to present difficulties in his views, but they seem to be in general accord. Thus the simplest types of coeno-gametes are found in the simpler groups of Phycomycetes and Ascomycetes, and the more complex conditions in forms above.

If coenogametes may lead up towards a heterogamous level of sexual evolution, their sexual organs, while closely resembling those of the algae, might not be strictly homologous. Thus the eggs of Saprolegnia and the Peronosporales do not seem to be the exact homologues of the eggs of any alga, and the female organ is unlike the typical oocyst because of obvious relations to coenogamete condi-tions. Their male organs differ from spermatocysts in their coeno-cytic behavior. Similarly the sexual organs of the Ascomycetes do not fall into the classification based upon the gametocyst. For these structures the old designations of oogonia, ascogonia (archicarps), and antheridia are applicable, and they will be thus distinguished from the two main classes of sexual organs, the gametocysts and gametangia.

### IV. SUMMARIZED LIST OF THE SEXUAL ORGANS OF PLANTS.

This summary presents the new terms introduced in our discussion of the sexual organs of plants. As stated in the beginning of the paper, the establishment of a terminology is a matter of usage; its importance will rest entirely on the value of the classification and its ability to express the characteristics. These new terms will interest chiefly the morphologist who seeks to understand and express rela-tionships. Much of the work of taxonomy disregards difficult prob-lems of morphology, and in this subject the older descriptive terms (oogonium, antheridium, sporangium, etc., among the thallophytes) are sure to be used, in some cases without regard to the exact homol-ogies of the organs considered.

*Sporocysts* are unicellular structures developing asexual spores.

*Gametocysts* are unicellular structures developing uninucleate gametes. These are the most primitive types of sexual organs and are derived from *zoosporocysts*, unicellular structures that develop zoospores. Gametocysts become sexually differentiated into

*Spermatocysts*, unicellular structures developing sperms, and

*Oocysts*, unicellular structures developing eggs.

*Gametangia* are multicellular organs which develop uninucleate gametes. These are believed to be derived from zoosporangia, multicellular structures which form zoospores. According to the author's hypothesis (DAVIS '03 *c*) the gametangia of groups of extinct Chlorophyceae leading into the bryophytes became differentiated into

*Spermatangia* (antheridia), multicellular organs developing sperms, and

*Oangia* (archegonia), multicellular organs developing eggs.

*Coenogametes* are multinucleate sexual cells, and are morphologically either gametocysts that have become changed directly into gametes, or they are restricted portions of such cells. In the Mucorales and Gymnoasceae the coenogamete contains all of the protoplasm of the parent cell. In the Peronosporales and certain Ascomycetes only a portion of the protoplasm of the gametocyst is utilized in the gamete, the superfluous protoplasm passing into sterile structures (periplasm, conjugating tubes, sterile cells, etc.). The sexual organs of these latter forms, which are probably higher conditions than the former, may very properly retain the old names of oogonium, ascogonium, and antheridium. The structure of the sexual organs of the lichens and the Laboulbeniaceae is not sufficiently known to establish their position in this classification.

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# A LICHEN SOCIETY OF A SANDSTONE RIPRAP.

## BRUCE FINK.

### (WITH FIVE FIGURES)

THE ecologic conditions governing the composition of a given lichen society are interesting and instructive, though often difficult to determine with any degree of certainty. The writer has in various papers attempted to trace in a general way some of these conditions, treating a considerable number of societies and attempting to show how the plants are adapted structurally. Among other societies thus studied, there are a number occurring on sandstone, all surrounded by very similar climatic but quite different edaphic conditions. Some of these societies of the sandstones are surrounded by other lichen societies, usually of trees, and show most interesting instances of tension lines and invasions of certain lichen species from one to another of two adjacent societies. Discussions of these societies may be found in the writer's papers concerning the lichen floras of Minnesota and Iowa.

## I. DESCRIPTION OF THE RIPRAP.

The lichen society to receive special attention in this paper is peculiar in a number of ways. For some time it has seemed desirable to study other lichen societies of sandstone than those of ledges along streams, and advantage was taken of the first opportunity for such an investigation far from a large stream by taking a society found growing upon rocks removed from their native beds. Before considering the society, it will be in order to state its location and to explain something of the surrounding conditions and antecedents which have made its existence possible. The riprap on which the society occurs forms a brace and a protection for a high grade of the Rock Island railroad, four miles west of Grinnell, Iowa. The rock of which the riprap is constructed is the ferruginous sandstone of the lower Carboniferous, and was obtained at Kellogg, some thirty miles westward on the same railroad. The riprap lies on the north side of roadbed, and is in the form of a wall along the upper part of the grade

and four bracing extensions running downward and away from the track, nearly to the base of the high grade (*fig. 1*). The riprap wall, running parallel to the roadbed and $1.2^m$ below it, is $60^m$ long, varies from 1.5 to $2.5^m$ in perpendicular height, and rises at an angle of 45 to 55°. The four bracing extensions run down the sides of the grade at right angles with the wall above and at an angle of about 30°. The length of the extensions averages about $21^m$, and they vary from 2 to $2.7^m$ in width. A grass-sedge swamp lies to the north of the



FIG. 1.—View of a portion of the northward-exposed wall and portions of two of the extensions, showing something of the spermatophytic flora and the general plan of structure of the riprap.

society and contains a considerable amount of water in wet seasons. The vertical height of the grade above the swamp level is about $12^m$, and the riprap extensions pass from within $1.2^m$ of the track bed, downward to within $3^m$ of the swamp level. The riprap was built in 1874 and is thus thirty years old.

## II.  ECOLOGIC FACTORS.

The conditions as a lichen-bearing substratum are unique in a number of ways. Though the same rocks used for walls under buildings and ten or more years older are apparently sound, the loosely

laid and more exposed rocks of the riprap have weathered considerably and differentially, the rate of weathering depending partly upon position and in part upon the amount of cementing iron contained in each particular piece.   In its position away from running water, a portion of the disintegrating sand of the riprap remains on the ground and in the crevices and forms a small amount of soil upon which plants may grow.   Again the riprap is partly swamp-bound, with woods some 150$^m$ away.   Also there are only two or three bowlders near by, the Kansan drift which covers the surrounding country carrying very few at the surface.   Thus there are at present and have been since the establishment of the society no lichens, or at least none that can be detected readily, in the region immediately surrounding the society; for one would hardly look for lichens among the plants of the grass-sedge swamp or among the xerophytic spermatophytes of a gravelly railroad bed worked year after year.   Hence we have here an isolated lichen society, which has developed to its present condition during the last thirty years, while separated from the nearest lichen society by 150$^m$.

How each individual species of the society found its way to the spot cannot now be ascertained certainly.   Indeed, one well acquainted with lichens might pass the spot without examination, so complete is the isolation of the society and so barren do the rocks appear at first inspection.   In fact it is only after an examination of the rocks with a hand lens and a careful survey of the crevices that anything of special interest is discovered.   Till recently cut, a group of oaks and other trees were standing about 150$^m$ distant from the riprap, and these trees bore the foliose Parmelias and Physcias, the fruiticose Ramalinas, and the crustose Placodiums, Lecanoras, and Rinodinas.   But the trees were young when cut, the largest measuring scarcely more than a foot in diameter and the majority about half this size, and were mere shrubs when the riprap was made, surely not carrying any of these lichens, except perhaps some of the crustose forms.   Were trees of good size and bearing lichens immediately surrounding the society, the lichens from the trees would now be gaining a foothold on the riprap blocks, though not so well adapted to the substratum as some other lichens.   Were numerous bowlders near at hand, another type of lichens might now be less sparingly represented in the

society.   But the lichens of the trees 150$^m$ away are on the whole of a type very sparingly represented on the riprap, those of the trees being of the genera mentioned above and very seldom seen on the riprap, and in the main then by different species, while those of the riprap society are mainly a number of crustose species absent from the trees or only sparingly represented on them, and several fruticose species wholly absent from the trees.   All of this will appear more plainly after a list of species of the society under consideration is given.   The causes which have led to the possession of the riprap by certain types of lichens may also be discussed to better advantage later, the intention here being merely to bring out the fact that proximity has not enabled the lichens of the trees to gain possession of the rocks in face of certain unfavorable conditions, and that other types have consequently gained the ascendancy.

As to moisture, the swamp brings an abundance of soil moisture, especially toward the lower ends of the riprap extensions.   Thus at certain times, as in wet seasons and after rains, the fruticose Cladonias grow well in the somewhat shaded and moist openings between the blocks of riprap, and pass into the desiccated condition without injury whenever the moisture becomes deficient.   Since the soil moisture does not pass upward through the loose riprap to any great extent, and the small blocks retain very little moisture, the upper surface of the sandstone blocks becomes drier than would the upper surface of a similarly exposed solid wall or natural exposure of the same kind of rock.   Accordingly the conditions on the upper surfaces of the extensions are quite xerophytic, especially toward the upper portion of each extension where farthest removed from the swamp and where the vertical height of the extensions averages about 1.8$^m$. Passing downward on the upper surface of the extensions, as the height of each one gradually decreases and the soil becomes more moist, the soil moisture works upward through the riprap blocks more and more, so that the conditions become gradually less xerophytic.   Passing to other considerations for the present, the change in lichen species upon the upper surface, resulting from the varying ecologic conditions, will receive attention below.

The conditions determining the composition of the lichen society are plainly quite different, surely drier and doubtless on the whole

somewhat less varied than those affecting the seed-plants surrounding
the lichens.   Yet for those more accustomed to the considerations
of societies of these higher plants, a brief statement of the types of
seed-plants will be more illuminating than would a mere statement
of physiographic conditions and the corresponding structural adapta-
tions of the lichens.   So although the conditions affecting the lichens
are somewhat different, we will no doubt be able to consider the lichen
society more intelligently after such brief view of the higher plants.
On the upper surface of the extensions and along the northward-
facing riprap wall, the xerophytic conditions are plainly seen in the
few scattered seed-plants, including *Onagra biennis, Lepidium inter-
medium, Ambrosia artemisiaefolia, Cassia chamaecrista, Hordeum juba-
tum, Polanisia trachysperma, Polygonum scandens, Verbascum Thapsus*,
and *Cenchrus tribuloides*.   The same xerophytes occur on the dry
gravel of the road bed with *Equisetum arvense, Chenopodium Botrys*,
and one or two others; and in passing downward one encounters
dry meadow, wet meadow, and grass-sedge swamp conditions, all
in the few meters, the hydrophytic flora of the swamp showing a num-
ber of large grasses and sedges, *Cicuta maculata, Typha latifolia*,
*Alisma Plantago, Scirpus lacustris*, some forms of Sagittaria, and a
number of fresh water algae in the limited areas where water stands
a larger part of the time.

### III. COMPOSITION OF THE LICHEN SOCIETY.

That such rapid transition in seed-plant flora should be accom-
panied by somewhat similar conditions in the lichen flora would be
expected; but the riprap does not extend down to the swamp, and
the lichens either do not grow on the soil, or when they do they have
in their rhizo·ds poor means for seeking moisture as compared with
the somewhat fleshy and deep-growing roots of some of the xerophytic
seed-plants named above.   Hence the lichens are not so much affected
by the conditions as to soil moisture as are the seed-plants.   Accord-
ingly the moisture-loving Collemas, Leptogiums, and Pannarias are
entirely absent.   The extreme xerophytic adaptation as to lichen flora
is shown in *Biatora myriocarpoides*, which grows abundantly on the
driest portions of the upper surfaces of the riprap extensions, this
plant representing in the more xerophytic lichen society what the

xerophytic seed-plants named above do in the spermatophytic society. The lichens composing the society, naming the genera in the order of the importance of one or more of their species as floral elements of the society, are as follows:

*Biatora myriocarpoides* (Fr.) Tuck. (*Lecidea salvicola* Flt.), the most common lichen of the society, and most abundant on the driest and most exposed portions of the riprap extensions; appearing as dark stains on the rocks, the nature of which can only be ascertained with hand lens.

*Bacidia (Biatora) inundata* (Fr.) Kbr., replacing the last above to some extent in the more moist and shaded portions of the society, both on rocks and soil, the plant being as the name indicates somewhat hydrophytic in nature. This species also occurs sparingly mingled with the last in quite dry portions of the upper surface of the riprap extensions, where the thallus is more scanty than in its more natural habitat. The two plants, where occurring together, are very difficult to distinguish macroscopically.

*Cladonia mitrula* Tuck., on earth and rock along the northward-facing wall; frequent; rarely on the extensions.

*Cladonia cariosa* (Ach.) Spreng., on soil from disintegrated and somewhat shaded rock; rare.

*Cladonia cristatella vestita* Tuck., on more or less disintegrated rock and usually on the lower and more moist portions of the riprap where more or less shaded; rare.

*Cladonia furcata* (Huds.) Schrad.; only one well developed plant seen and that in a well protected and moist place on the east basal part of the upper portion of one of the riprap extensions.

*Cladonia fimbriata coniocraea* (Flt.) Wainio, in shaded or somewhat exposed places and more often toward the moist basal portions and sides of the riprap extensions; quite frequent; hitherto reported in Iowa under the varietal name *tubaeformis* Fr., which has also included the next.

*Cladonia fimbriata apolepta* (Ach.) Wainio, with the last, but rare and difficult to distinguish.

*Cladonia fimbriata simplex* (Weis.) Wainio, in well shaded spots; rare; new to Iowa, and easily confused with the second below, from which it differs in its more slender habit, its more sorediate condition, and its tendency to pass into the irregularly cylindrical forms of the last two above.

*Cladonia pyxidata neglecta* (Flk.) Schaer., in more or less damp and shaded places on disintegrating rock; frequent.

*Cladonia pyxidata chlorophaea* (Spreng.) Flk., in more or less shaded places toward the base of the riprap extension; rare. These two varieties have not previously been recognized in Iowa collections.

*Cladonia gracilis dilacerata* Flk., on shaded or northward-facing and more or less disintegrated surfaces: rare

*Cladonia gracilis dilatata* (Hoffm.) Wainio, occurring with the last; rare. These forms have not been recognized before in Iowa, but have been included under the partial synonym var. *hybrida* Fr.

*Stereocaulon paschale* (L.) Ach. (?), on exposed and little disintegrated rock, but better developed toward the basal, damp, and more disintegrated portions of the riprap extensions. Small and perhaps as near *S. coralloides*. A northern species new to Iowa. Frequent, but only once seen in fruit.

*Lecanora cinerea* (L.) Sommerf. (?), on exposed and comparatively firm rock; once seen and sterile.

*Lecanora muralis saxicola* (Poll.) Schaer., occurring as the last; once seen and sterile.

*Placodium aurantiacum* (Lightf.) Naeg. and Hepp, on firm rock of the riprap wall; once seen.

*Placodium vitellinum* (Ehrh.) Naeg. and Hepp, on firm and exposed rock; rare.

*Placodium cerinum* (Ehrh.) Naeg. and Hepp (?), occurring as the last and rare; spores immature.

*Acarospora (Lecanora) cervina fuscata* (Schrad.) Fink; once seen on firm rock of the northward-facing wall.

*Acarospora (Lecanora) xanthophana* (Nyl.) Fink, on exposed and firm rock; once seen and sterile.

*Rinodina sophodes* (Ach.) Kbr.; once noted on a firm and exposed spot where the rock was especially hard because of the presence of a large amount of iron. In rapid field work the plant is not easily distinguished from the first of the list and may be somewhat more common than appears at present.

*Lecidea enteroleuca* Ach., on exposed rock, rare and easily passed over for the first of the list.

*Verrucaria muralis* Ach., on exposed and comparatively firm surfaces; rare.

*Verrucaria fuscella* Fr., occurring with the last and more rare.

*Parmelia Borreri* Turn., on quite firm, but somewhat damp and shaded rock; rare and sterile.

*Parmelia conspersa* (Ehrh.) Ach., occurring as the last and also very rare and sterile.

*Physcia stellaris* (L.) Tuck., once seen on the shaded, northward-exposed wall.

*Ramalina calicaris* (L.) Fr., on damp surfaces toward the base of the northward-facing wall; once seen.

*Dermatocarpon (Endocarpon) pusillum* Hedw., on somewhat shaded rocks of one of the riprap extensions; very rare.

Besides the thirty forms listed above, there occurs commonly a sterile thallus somewhat like that of *Amphiloma (Pannaria) lanuginosum (fig. 2)*. This thallus is without distinct cortex and seems nearly as rudimentary as that of Amphiloma, but is verrucose rather

than finely granular, is chinky or subareolate and not so distinctly
sorediate as the thallus of Amphiloma.   This unknown thallus seems
also to resemble that of *Urceolaria scruposa* in microscopic structure,
but it is not so well developed.   This lichen is a very conspicuous
feature of the society and is common toward the basal, damp ends
of the riprap extensions, especially the eastward two.   It also extends
upwards to the upper end of the extensions, but in passing upward
is confined more and more to the damp sides and crevices.
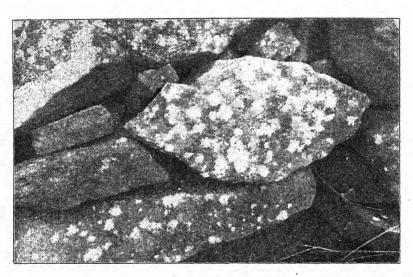


Fig. 2.—Blocks of riprap at the side of one of the extensions, showing thalli of the
Amphiloma-like lichen.

### IV.   TYPES OF THALLI REPRESENTED.

As to types of lichen thalli in the society, we have in the main the
rudimentary type with leprose or finely granular surface and devoid
of cortex, and the fruticose cylindrical type with protective and
strengthening pseudocortex of mostly parallel and longitudinal
hyphae.   Other types, as the foliose and the areolate or squamose
corticate-crustose forms, appear but rarely and do not form a conspicu-
ous portion of the society.   The first type of thallus is represented
by the first two lichens of the list, and by the Amphiloma-like thallus.
The first, *Biatora myriocarpoides*, was doubtless the first lichen to

gain possession of any considerable portion of the riprap and is still abundantly maintaining itself in the drier places where the rock is not disintegrating so rapidly. The second of the list, *Bacidia inundata,* occupies similar but moister surfaces of both wall and extensions, its thallus varying considerably according to conditions of moisture, being well developed in the moist places where the species is usually found, but almost wanting in the dry, exposed places. These two species seem to prevail here instead of the better developed types of crustose thalli, because the rock disintegrates too rapidly for the possibility of extensive establishment of the better developed thalli. The better developed crustose thalli are the forms that prevail on such hard rocks as the Sioux quartzite, or as we shall see shortly, on riprap of similar sandstones where drier and disintegrating more slowly, and are represented in the present society by the rare specimens of Lecanora, Placodium, and Acarospora. A hasty study of the similar thalli of the Biatora and the Bacidia above named scarcely reveals definitely why one should be more xerophytic than the other, though the thallus of the former is on the whole more closely adnate than that of the latter. However, the Biatora shows under the microscope a more pronounced xerophytic adaptation in the somewhat tougher, more lecideine condition of the hypothecium and exciple, and in the somewhat better development of the para-physes.

The cylindrical type of thallus is represented by the Cladonias and by the single species of Stereocaulon. These lichens thrive best in the society where they may have a fair supply of moisture and shade, when somewhat protected from the wind, and on soil, or on rocks somewhat disintegrated. The conditions as to moisture, shade, and protection from wind are all fairly well met in the crevices toward the base of the northward-facing wall, in the openings between riprap blocks, and in certain places protected more or less by a projecting block. As has been stated, these plants are often able to maintain themselves in spite of disintegration, and when the product of dis-integration remains *in situ* are actually invigorated by the process and finally come to rest on a sandy soil

V.  VARYING ECOLOGIC CONDITIONS AND RESULTING DISTRIBUTION
OF MEMBERS OF THE SOCIETY.

Plainly the conditions on the upper surface of the riprap extensions become less xerophytic n passing downward toward the swamp below, and also because the riprap is not so high toward the lower ends.  The gradual increase in amount of moisture influences perceptibly the distribution of the lichens upon the riprap extensions. *Biatora myriocarpoides* is more prevalent toward the upper portion of each extension, not because it is poorly adapted to the more moist conditions farther down, but because in the latter position the plant must compete with others as well or better adapted to the position. The Amphiloma-like  hing, in its distribution upon the riprap, shows a most delicate adjustment to conditions of moisture.  At the lower ends of the extensions it is more common, rises to the exposed surface and forms a conspicuous portion of the flora; while in passing upward, it becomes less and less conspicuous, and toward the upper ends is scarcely noticeable on the exposed upper surfaces of the blocks, but is frequently seen in crevices and increasingly so the deeper one may be able to look downward through the loose riprap. *Bacidia inundata* occurs on the northward-facing wall and competes with the last for position upon the upper surface toward the lower ends of the extensions, but from its inconspicuous character and less frequent occurrence does not form so conspicuous a portion of the society.  The Cladonias also are most delicately responsive to moisture conditions in their distribution in the society (*fig. 3*).  Toward the lower ends of the extensions, they rise to the exposed surfaces of the riprap, and in passing upward are more and more inclined to seek the more moist and shaded positions in the cracks between the blocks of riprap and along the sides of each riprap extension or toward the base of the wall.  It has already been noted that less moisture reaches the upper surface toward the upper ends where the extensions are higher, and it may be added here that these same surfaces are more exposed to the drying winds than those at the lower ends of the extensions and nearer the level of the general surrounding surface, this condition also influencing the distribution of the Cladonias.

VI.   ORIGIN OF THE SOCIETY.

Just how each species arrived at the spot or when it came is not easily stated.   It is supposed that fragments of lichens carried in the wind fall in places favorable for growth.[1]   Few of the lichens of the society are conspicuously sorediate, but it is probable that nearly all of them arrived at the spot from some place near at hand, through purely vegetative dissemination.   In this way the species may even
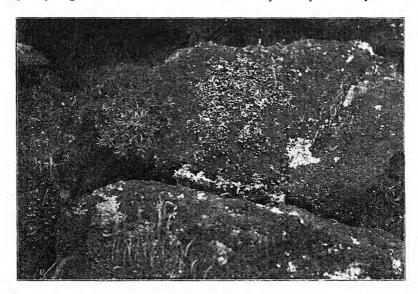


FIG. 3.—Somewhat shaded and disintegrated riprap blocks near ground on north side on an extension, with *Cladonia fimbriata* scattered throughout the field, *C. furcata* at the left, *C. cristatella vestita* in the crevice at the forefront, and a few white thalli of the Amphiloma-like plant.

have arrived from stations quite remote from their present position. Taking into account the statements given above as to the scarcity of lichens in the circle of 300$^m$ in diameter and immediately surrounding the society, this supposition seems quite probable, at least for quite a number of the species.   Yet the inconspicuous, crustose species may have come from a few Kansan bowlders recently removed. Thus the Biatora and the Bacidia may have reached their present

[1] PEIRCE, G. J., The nature of the association of alga and fungus in lichens.   Proc. Calif. Acad. Sci. III. 1:213. 1899.

habitat, and the same may be stated regarding the rarer crustose members of the society, such as the Lecanoras, the Placodiums, the Acarosporas, the Verrucarias, the Rinodina, and the Lecidea. Yet a few of these crustose forms may have come from the trees some $150^m$ away, some of the trees no doubt being old enough to bear these lichens at the time when the riprap was built or shortly after. These species are the first and the last Placodium of the list, the Rinodina, and the Lecidea. As to the C adonias, there are not any conspicuous Cladonia-bearing substrata within a mile, except the loess and Kansan drift of railroad cuts, on which the first Cladonia of the list is very common. However, all of the Cladonias except *C. furcata* have been found within a few miles of the society, and in all probability arrived from various places not far away. The northern Stereocaulon, not known elsewhere in Iowa, doubtless originated in the society through fragments of thalli brought to the spot on railroad cars, and very probably on ties or telegraph poles. It is not so common a member of the society as a number of the similarly constructed Cladonias, and is usually found on the more solid rocks, the more disintegrated spots having been previously occupied by other lichens or mosses, and the rocks on which it occurs not having had time to disintegrate conspicuously since its advent into the society. The fact that the Stereocaulon (*fig. 4*) is almost uniformly sterile may indicate either that it has only recently gained access to the society, or that it is poorly adapted to the climatic conditions of the region. Also the position of this species on the northward exposure is worthy of note. The Ramalina, the Physcia, and the first Parmelia doubtless came as fragments from trees from one to several miles away, unless these rare members of the society may be thought to have come from fragments blown from the trees some $150^m$ away, since the trees became large enough to bear these species.

Before leaving this subject it must be pointed out that it is by no means a matter of chance what species will reach such an isolated lichen society and survive. But the matter is determined in such an instance largely by adaptability and early access before the substratum is occupied. As has been noted elsewhere, in instances where rock-lichen societies are adjacent to tree-lichen societies, the lichens of the trees, though scarcely so well adapted to the rocks,

because of proximity, get possession often of considerable portions of the rocky substratum.   Excepting the Stereocaulon, there seems to have been in the present instance a pretty nearly equal struggle for place in the society, those lichens that are best adapted to the ecologic conditions gaining the ascendency, and entirely or nearly completely crowding out those less well adapted.   That gaining possession is by no means a matter of pure chance will appear in the discussion next below of an adjacent society of a southward exposed riprap.



FIG. 4.—*Stereocaulon paschale* on a riprap block on the upper surface and toward the base of one of the extensions.

The Amphiloma-like thallus has been purposely omitted from these considerations of origin of the floral elements of the society, since no very definite statement can be made till the species is ascertained.

VII.   COMPARISONS WITH OTHER SIMILAR SOCIETIES.

A.   *The society of a neighboring riprap.*

There are a number of ripraps at various places along the south side of the railroad bed, and all of these have been examined, as well as others on the north side, the one selected for the present study

being by far the most extensive and the best one for such an investigation. For a comparison of the effect of north and south exposures, we may select a smaller riprap, consisting of a single extension, and lying directly across the track from the one on which occurs the society studied above. Indeed, the plants of the single extension on the south side of the track might perhaps be considered a portion of the society on the north side, but it was thought a separate consideration of them would better show the marked difference in character of the flora. The single extension is of about the same length and width as each one of the four on the north side of the track and makes about the same angle. The land to the south of the track is a low meadow with conditions distinctly less moist than in the swamp to the north. Yet more pronounced is the drying effect of southward exposure, and altogether we have distinctly more xerophytic conditions on this single riprap extension on the south side of the track. Plainly less shade is to be found on the southward exposed extension, and as a result of drier conditions the riprap blocks are much less disintegrated than those on the north side. A discussion of the species of lichens on the riprap south of the railroad track will demonstrate a remarkably nice adjustment between lichen structures and ecologic conditions. The species are as follows:

Acarospora xanthophana (Nyl.) Fink, scarcely infrequent; A. cervina fuscata (Schrad.) Fink, frequent; A. cervina cinereoalba Fink, frequent; Biatora myriocarpoides (Fr.) Tuck., rare; Buellia myriocarpa (DC.) Mudd, frequent; Verrucaria fuscella Fr., frequent; Lecanora muralis Ach., infrequent; L. subfusca (L.) Ach., rare; Placodium cerinum (Ehrh.) Naeg. & Hepp, scarcely infrequent; P. vitellinum (Ehrh.) Naeg. & Hepp, rare; Parmelia conspersa (Ehrh.) Ach., once seen in a somewhat protected spot; Cladonia fimbriata coniocraea (Flt.) Wainio, once seen in a protected and shaded spot.

Besides the above, the Amphiloma-like plant is sparingly found on this southward-exposed extension, occurring in shaded spots and especially toward the base, where it is sometimes in more exposed positions. Comparing the lichens of the list above with those of the list for the northward-exposed riprap across the track, we find that the general structure of the plants in the two societies is very different. *Biatora myriocarpoides*, abundant on the north side, is rare on the south side; and the Acarosporas, each once seen on the north side, are all frequent on the south side. In the more xerophytic conditions of

the southward exposure, *Buellia myriocarpa* has in part replaced
the Biatora. The better adaptation of the Buellia appears in the
greater tendency toward disappearance of the thallus and the better
development of such protective structures as exciple, hypothecium, and
paraphyses. The Biatora is further replaced by the Acarosporas.
This is due to two causes. Primarily, the disintegration being
slower on the drier southward-exposed riprap, the more highly
developed thalli of the Acarosporas have time for development and
the production of apothecia on the more permanent rock surfaces,
and are consequently frequent and often fruited. Secondarily, with
their well-developed upper cortices the Acarosporas are even more
able to endure extreme xerophytic conditions than is the Biatora.
Also *Lecanora muralis*, once seen on the north side, was noted several
times on the south side, where thalli with well developed cortices
are better adapted to the conditions. Response to conditions is
beautifully shown in that while Cladonias are common enough on
the moister and more shaded north side, only a single specimen could
be found on the south side. Also the total absence of the Stereo-
caulon from the southward exposure is quite significant, especially
when we recall that it occurs commonly in quite exposed places a
few meters away on the north side. Finally, the response of lichens
to conditions of environment, as shown here, is quite remarkable
and fully justifies the detailed attention to a limited area.

### B.   *The society of the sandstone ledges near Boone, Iowa.*

The types of lichen structure found in the societies of other sand-
stone exposures studied in Iowa and Minnesota have been quite
different. The places studied have been ledges along streams, which
have for the most part either carried away the loose sand as fast as
the rocks were disintegrated, or frequently subjected it to inundation,
which few foliose or fruticose lichens will endure. In such societies,
almost the only Cladonias found have been those growing on the
faces of the ledges, while in the present society some of the products
of erosion have remained to make a soil in which these lichens could
grow. The study of a ledge along a stream was recently carried out
more completely at the "Ledges" (*fig. 5*) in Boone county, Iowa,
than the writer has done elsewhere; and while the study of the col-

lection made at the "Ledges" is not yet completed, enough has been done so that data for comparison are at hand. The "Ledges" have an extent of about two miles along a tributary of the Des Moines river and are fully 15$^{m}$ high in some places. They are well shaded in many places and bear a higher plant flora quite different from that about the society especially studied above, and including such moisture-lovers as *Camptosorus rhizophyllus, Woodsia obtusa, Asarum canadense, Impatiens aurea, Anemone quinquefolia, Arisaema Dracontium, Adicea pumila, Aralia racemosa, Conocephalus conicus,* and a species of Grimaldia or Preissia; while the conditions at other points are more xerophytic and bear a number of ferns, composites, and trees or shrubs. The lichen species of the "Ledges" are for the most part quite widely distributed upon the rocks, so that the whole number recorded is about the same as for the riprap. The list is as follows:

Usnea barbata Fr., infrequent; Ramalina calicaris farinacea (L.) Fr., frequent; R. calicaris fastigiata (Pers.) Fr., infrequent; Parmelia Borreri Turn., common; P. crinita Ach., frequent; P. caperata (L.) Ach., infrequent; Physcia pulverulenta (Schreb.) Nyl., infrequent; P. speciosa (Wulf.) Nyl., rare; Peltigera canina (L.) Hoffm., frequent; P. canina spuria (Ach.) Tuck., rare; Senechoblastus (Collema) nigrescens (Ach.) Stizenb., rare; Collema pulposum (Bernh.) Ach., rare; Leptogium chloromelum (Sw.) Nyl., infrequent; Pannaria nigra (Huds.) Nyl., common; Amphiloma (Pannaria) lanuginosum (Ach.) Nyl., abundant; Acarospora (Lecanora) fuscata oligocarpa Nyl., rare and new to Iowa; Lecanora muralis (Schreb.) Schaer., rare; Placodium aurantiacum (Lightf.) Naeg. & Hepp, frequent; P. cerinum (Ehrh.) Naeg. & Hepp, infrequent; P. vitellinum (Ehrh.) Naeg. & Hepp, frequent; P. citrinum (Hoffm.) Leight., rare; Pertusaria velata (Turn.) Nyl., rare; Urceolaria scruposa Ach., rare; Cladonia mitrula Tuck., common; C. caespiticia (Pers.) Flk., rare; C. pyxidata chlorophaea (Spreng.) Flk., frequent; Bilimbia (Biatora) trachona (Flt.) Fink, rare; Buellia spuria (Ach.) Arn., rare; Dermatocarpon (Endocarpon) pusillum Hedw., common; Verrucaria muralis Ach., common; V. nigrescens Pers., frequent; V. viridula Ach., rare and new to Iowa; V. fuscella Fr., rare.

A comparison of the list above with that for the riprap shows little resemblance. The most striking difference is the occurrence of the shade- and moisture-loving lichens in the society at the "Ledges," which are absent from the riprap society. These shade-loving lichens are the Collemas, the Leptogium, the Pannaria, and the Amphiloma. The next most conspicuous difference is that on the

solid and less rapidly disintegrating surfaces at the "Ledges," the somewhat better developed crustose thalli, as the Lecanoras, the Placodiums, the Pertusaria, the Urceolaria, and the Buellia, have to some extent replaced the less differentiated thalli such as the first two of the list for the riprap. Because the disintegrating sandstone of the "Ledges" falls to the ground and is covered with water
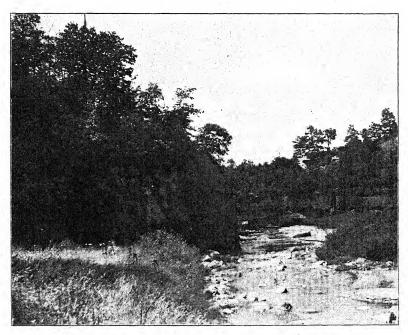


Fig. 5.—Portions of the "Ledges" on both sides of the stream, showing general features and spermatophytic flora.

and partly carried away in high water, the Cladonias appear only on the sandstone of the ledge faces and are comparatively rare. The more frequent occurrence of the foliose Parmelias and Physcias and the fruticose Ramalinas at the "Ledges" is due partly to the more shaded and moist conditions, and in part to the presence of surrounding trees, from which they may easily wander to the rocks. The above comparison of the two societies is the more interesting when it is stated that both are growing upon the ferruginous sandstone of the same geological horizon, and that the differences noted

are not due in any degree to difference in rock composition, but entirely to other ecologic factors.

### C. *Some other similar societies.*

The lichen societies of various other sandstones differ somewhat from either of the two considered above. Of those hitherto considered, only a single one, that of the Sioux quartzite at Pipestone, Minnesota, is isolated in such a way as to show no tension lines or admixture of elements that so frequently intrude themselves from other adjacent lichen societies. The lichens that have established themselves here are a number of Acarosporas, Placodiums, Lecanoras, Rinodinas, and Buellias. These lichens in general have strictly crustose thalli, well developed and variously chinky, verrucose, and areolate, and some of them at least a well developed upper cortex. With these, two foliose but closely adnate Parmelias and two similar Physcias occur here and there in the society, but do not form a conspicuous portion of it. Much of the beautiful wind polishing of the quartzite was surely done at latest before the Wisconsin stage of the Pleistocene, or shortly after the retreat of the Wisconsin ice, and the writer finds the lichens growing on the smoothly polished surfaces, which are as much polished below the lichens as elsewhere. Thus there has been no visible change in the surface of the quartzite since the advent of the present lichen society, and these lichens with well developed thalli have had an abundance of time in which to become established upon the hard surfaces. There is no doubt but that these species may reach an advanced age upon the quartzite, becoming much older than is possible upon the more rapidly eroding ferruginous sandstone of the riprap, and the finding of all the species in good fruit upon the quartzite is quite conclusive evidence of considerable age. No doubt many of these lichens of the quartzite were growing when the riprap was built. Yet we find mainly the same species upon the southward exposed riprap extension, and this shows that such thalli may become established upon the softer sandstone in a comparatively short time.

[2] FINK, B. Contributions to a knowledge of the lichens of Minnesota. V. Lichens of the Minnesota valley and southwestern Minnesota. Minn. Bot. Studies **2** : 284. 1899.

Neither upon the softer sandstone nor upon the harder quartzite has the writer been able to observe any certain evidence of the protection which the lichens have afforded the rocks against wind or other atmospheric agencies, though other observers find such evidence elsewhere on rocks of the same kind.[3]    But whether the acidic action of the lichen thalli upon the rocks, or the climatic, erosion-producing agencies acting upon the surrounding rocks causes the more rapid disintegration, in the end the two factors together act on the softer ferruginous sandstone with comparative rapidity; and as compared with the lichen population of the quartzite, that of the sandstone is quite transient, lichen thalli or portions of thalli disappearing and becoming replaced, except upon the southward exposed extension, more rapidly than the better developed thalli can become established and produce fruit.   So it happens that when lichens having the better developed thalli are found, as they rarely are, in the society especially considered in this paper, they are likely to be sterile; while those with less differentiated and apparently more rapidly developing thalli are the ones that are common and well fruited.    The fruticose species, as the Cladonias and the Stereocaulon, are rather rarely established upon the firmer and more exposed rocks.    In their more or less shaded and moist habitat in the holes in the riprap, or in protected places about the basal blocks, these fruticose species are able to maintain themselves in spite of disintegration, the wind not blowing them away as is the fate of the smaller thalli on the more exposed surfaces, as soon as these thalli and the atmospheric agencies together disintegrate the rocks sufficiently.   Finally, any of the fruticose forms that attempt to gain a foothold on the more exposed surfaces are probably even more likely to be blown away as disintegration proceeds than are the crustose forms, though the rhizoids of the former penetrate the rocks to greater depth than do the hyphal rhizoids of the latter.

The lichen societies of the Saint Peter sandstone along the Mississippi River at Minneapolis and south of McGregor, Iowa, have been considered in a previous paper[4], and are quite different from the one discussed chiefly in this paper; and the same may be said of the

3 SHIMEK, B, Living plants as geologic factors.   Proc. Iowa Acad. Sci. 10 : 42.  1902.

4 FINK, B., Notes concerning Iowa lichens. Proc. Iowa Acad. Sci. 5 : 180.  1897.

society of the similar Jordan sandstone near Mankato, Minnesota.[5] However, these last three societies were not so exhaustively studied as the first three considered, and a further examination would bring to light some of the less conspicuous members of the societies and decrease the apparent differences.

### VIII. CONCLUSION.

The facts stated show clearly some very evident adaptations in lichen thalli, and as disintegration is going on with comparative rapidity at the spot where the society is found, the data herein established will be found useful in future studies. Finally, it may appear that undue attention has been given to a society covering a limited amount of surface. However, as the writer has stated elsewhere,[6] it is impossible to deal with the details of the ecologic distribution of lichens over a large area, and he has purposely chosen to restrict himself, as in this instance, so that certain minute details might receive attention.

Thanks are due Dr. L. H. Pammel for a photograph of the "Ledges."

IOWA COLLEGE, GRINELL, IOWA.

[5] FINK, B., Contributions to a knowledge of the lichens of Minnesota: V. Lichens of the Minnesota valley and southwestern Minnesota. Minn. Bot. Studies 2 : 301. 1899.

[6] FINK, B., Ecologic distribution an incentive to the study of lichens. The Bryologist 5 : 40. 1902.

# TRANSPIRATION OF SUN LEAVES AND SHADE LEAVES OF OLEA EUROPAEA AND OTHER BROAD-LEAVED EVERGREENS.

Joseph Y. Bergen.

(WITH ELEVEN FIGURES)

THE structural differences between sun leaves and shade leaves of several species have been described in a classical memoir by E. STAHL.[1] FR. JOHOW has given an excellent summary of the adaptations of foliage leaves with reference to transpiration.[2] LEON DUFOUR has investigated many of the differences in the vegetative and the reproductive organs of phanerogams due to differences in the amount of light supplied to them.[3]

The writer has not at present access to any tolerably complete collection of botanical periodicals, but neither in ALFRED BURGERSTEIN's bibliography[4] nor in such journals as were accessible has he been able to find mention of any paper which discusses experimentally the subject of transpiration *in leaves of the same individual*, some developed in the sun and others in the shade. It would seem that the study of the relative activity of sun leaves and shade leaves must give results of value. For such an investigation no leaves can be more suitable than those of such evergreens as the Mediterranean species of what Schimper calls the *Hartlaubflora*, Olea, *Quercus Ilex*, Myrtus, and their congeners. For it is evident that leaves which are active during a period of from one to several years, and which during all of that period are respectively exposed to illuminations varying from 2 per cent. to 100 per cent. of the total amount afforded by the sun, may be expected to show far more notable differences in structure

[1] Einfluss des sonnigen oder schattigen Standortes auf die Ausbildung der Laubblätter. Jena. Zeits. Naturwiss. **16**:162. 1882.

[2] Ueber die Beziehungen einiger Eigenschaften der Laubblätter zu den Standortsverhältnissnissen. Jahrb. Wiss. Bot. **15**:—. 1884.

[3] Influence de la lumière sur la forme et la structure des feuilles. Ann. Sci. Nat. Bot. VII. **5**:311–412. 1887.

[4] Materialien zu einer Monographie der Transpiration der Pflanzen. Verhandl. Zoöl.-Bot. Gesells. Wien. 1887 and 1899.

and function, due to unequal illumination, than those leaves which flourish only for four or five months of the year. Broad-leaved ever-greens, too, cast a denser shade than is afforded by ordinary conifers, and the leaves of the former therefore grow under more sharply con-trasting conditions than do those of the latter.

The lack of suitable laboratory facilities has made it impossible for the writer to investigate the relative amounts of photosynthesis accomplished by the leaves of the species studied. It has been possi-ble, however, to determine with a fair degree of accuracy the relative amount of transpiration done by the sun leaves and the shade leaves of several species.

The trees and shrubs mostly studied were: *Olea europaea sativa*, *Pistacia Lentiscus*, *Quercus Ilex*, and *Rhamnus Alaternus*. The obser-vations, unless otherwise stated, were made upon leaves from thirteen to fifteen months old. Where sun leaves and shade leaves were compared these were from different parts of the same shrub or tree, those which received only part of the total illumination being shaded wholly by their own foliage.

### I. COMPARISONS OF COLOR, SIZE, SHAPE, AND STRUCTURE OF SUN LEAVES AND SHADE LEAVES.

Out of ten trees and shrubs examined with reference to the effect of illumination on the color of the upper surface of the leaf, only one, *Quercus Ilex*, showed sun leaves always darker than the shade leaves. In this species the sun leaves when fully matured were always found to be of a very dark green, while shade leaves (1 to 2 per cent. illumi-nation) were of a grass-green color.

*Buxus sempervirens* showed no perceptible difference in color due to difference in illumination.

Eight species (*Arbutus Andrachne*, *A. Unedo*, *Citrus Aurantium*, *Myrtus communis tarentina*, *Nerium Oleander*, *Olea europaea*, *Pis-tacia Lentiscus*, *Rhamnus Alaternus*) showed a much darker tint of green in the shade leaves than in the sun leaves, though sometimes the shade leaves of Pistacia are lighter green. The shade leaves in the individuals studied received amounts varying from 1 to 10 per cent. of the total illumination.

In comparing the relative areas of sun leaves and shade leaves,

the author arrives at a result opposite to that which DUFOUR[5] obtained from the study of many herbaceous species, but agreeing with the results of JOHOW.[6]

One species, *Nerium Oleander*, has leaves extraordinarily variable in size, the smallest being bractlike and only 0.027 the area of the largest ones.   It did not seem possible to make satisfactory estimates of the relative areas of the sun leaves and shade leaves of this species.

All other species examined had shade leaves larger than their sun leaves.   Exact measurements were made for only four species of these, as follows:

|  | Ratio of areas Sun ÷ shade |
|---|---|
| Citrus Aurantium | 0.75 |
| Olea europaea | 0.56 |
| Quercus Ilex (large tree) | 0.44 |
| Q. Ilex (small bushy sapling) | 0.20 |
| Rhamnus Alaternus | 0.68 |

The comparisons were based on fairly typical twigs of the same age, and all the leaves of each twig, or an equal number of homologously situated leaves from each, were examined.

The shapes of the two classes of leaves in question were often found to differ widely.   The ratio of length to breadth for the blades of the leaves was examined in ten species.   In the pinnately compound leaves of *Pistacia Lentiscus* there was little difference in the ratios of sun leaves and shade leaves, whether leaf was compared with leaf or leaflet with leaflet.   The other nine species gave the following results:

|  |  | Ratio length ÷ breadth | |
|---|---|---|---|
|  |  | Sun | Shade |
| (1) | Arbutus Andrachne | 2.70 | 2.35 |
| (2) | A. Unedo | 3.16 | 3.21 |
| (3) | Buxus sempervirens | 1.97 | 1.89 |
| (4) | Citrus Aurantium | 2.04 | 1.37 |
| (5) | Myrtus communis tarentina | 2.21 | 2.14 |
| (6) | Nerium Oleander | 5.90 | 5.34 |
| (7) | Olea europaea | 4.05 | 2.64 |
| (8) | Quercus Ilex (large tree) A | 2.69 | 1.60 |
|  | Q. Ilex (small bushy sapling) B | 2.04 | 1.37 |
| (9) | Rhamnus Alaternus | 1.75 | 2.05 |

[5] *Loc. cit.*, p. 351.      [6] *Loc. cit.*, p. 304.

It was not possible in every case to obtain the per cent. of total illumination for the shade leaves examined. Those noted were as follows: (4) 2.8, (6) 2.2, (7) 4.6, (8)A 1.8, (8)B 1.1, (9) 4.6.

It is obvious from inspection of the results obtained that the sun leaves are usually narrower than the shade leaves in proportion to their length. This is especially true of the leaves of Citrus, Olea, and Quercus; and the Olea and Quercus are certainly among the most xerophytic of the nine species in the list above given. *Figs. 1–5* sufficiently illustrate the difference in form of the leaves in question.
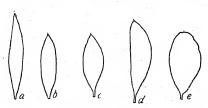


FIG. 1.—Leaves of *Olea europaea: A,* sun leaf of very xerophytic form; *B*, sun leaf; *C*, shade leaf from another tree; *D*, sun leaf; *E*, shade leaf from another tree which is in constant partial shade. ×0.4.

Another difference between the sun leaves and the shade leaves of many species consists in the manner in which the margins of the former are recurved. In many instances the under leaf surface of sun leaves is strongly concave, while that of shade leaves is nearly plane. This is well shown in the cross sections of *fig. 6.*

In the case of Olea the sun leaves and shade leaves differ remarkably in the manner in which they present their surfaces to the light. The latter are arranged in a somewhat horizontal manner, that is with the lower surface approximately parallel to the ground. But the former in many instances stand with the tips pointing almost straight upward or downward.
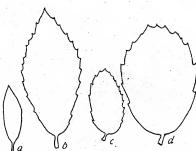


FIG. 2.—Leaves of *Quercus Ilex: A,* sun leaf, very small xerophytic form; *B*, shade leaf, same tree; *C*, sun leaf; *D*, shade leaf from another tree. ×0.4.

In other words, the shade leaves are approximately euphotometric and the sun leaves panphotometric. It does not appear that the edges of the leaves are presented in a north and south direction more frequently than toward other points of the

compass.    It is this approximately vertical position of many leaves, with the silvery under surfaces facing in all directions, that gives the shimmering effect of olive foliage so often described.  *Figs.* 7 and *8* illustrate extreme cases of leaves standing vertically as above described.[7]

The thickness of sun leaves was in every case found to be greater than that of shade leaves, as described by STAHL and others. In leaves of Quercus the ratio in thickness of the former to the latter was nearly 2.0; in Olea from 1.5 to 2.3; and in Pistacia from 1.8 to 3.7.
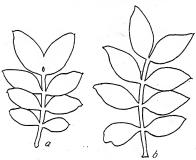


FIG. 3.—Leaves of *Pistacia Lentiscus:* A, sun leaf; B, shade leaf.  ×0.4.

In those species which are pubescent or scaly on the lower surface the pubescence is much denser on sun leaves.  It is generally difficult to reduce the comparison in this regard to a numerical basis, but an approximation of the kind can be made in the case of the leaves of Olea.   The lower surface of the leaf is always more or less completely covered with peltate scales.   On sun leaves the lower surface is so thickly scale-clad that the scales overlap considerably.

Apparently on sun leaves, the number of scales is sufficient to cover the under leaf-surface at least twice over.  On some shade leaves  the  scales  were found  by  measurements with  the  eyepiece  micrometer to cover just one-quarter of the under surface, so that the scales were about one-eighth as numerous as on sun leaves.
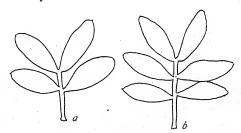


FIG. 4.—Leaves of *Pistacia Lentiscus* (another tree): A, sun leaf; B, shade leaf.  ×0.4.

The stomata were found to be somewhat more numerous on sun leaves than on shade leaves; an average of two determinations gave 15 per cent. excess for the former.

[7] For these drawings  the writer is indebted to Mrs. Herbert S. Jennings.

In none of the species studied were any such extreme differences between the internal structure of sun leaves and shade leaves noted as have been described by STAHL and others. Since the thickness and texture of the leaves of Pistacia differed more under different amounts of illumination than did those of any other species examined, special attention was paid to the histology of these leaves. The following points of difference, many of which can be verified by reference to *figs. 9–11*,[8] were made out: (1) cutinized layer of upper epidermis much more developed in sun leaves; (2) palisade layer double in sun leaves and single in shade leaves, the cells next the epidermis longer in the former; (3) intercellular spaces smaller in upper portions of mesophyll of sun leaves; (4) bundles much more highly developed in sun leaves; (5) a palisade layer occasionally developed next the lower epidermis in sun leaves.

FIG. 5.—Leaves of *Rhamnus Alaternus* and *Citrus Aurantium:*, *A*, sun leaf, and *B*, shade leaf of Rhamnus; *C*, sun leaf, and *D*, shade leaf of Citrus. ×0.4.

## II. RELATIVE AMOUNT OF TRANSPIRATION OF SUN LEAVES AND SHADE LEAVES.

The three most obvious cases which present themselves for investigation are: (*a*) transpiration of both kinds of leaves, each in its natural environment; (*b*) transpiration of both kinds in full sunlight; (*c*) transpiration of both kinds in shade.

No mode of determining the losses by transpiration of such leaves as those in question is free from sources of error. The plan of weighing detached leaves, with the cut end of the petiole sealed to prevent accidental loss, is an admirable one for succulent leaves. But for leaves with a less amount of stored water it is undesirable, because
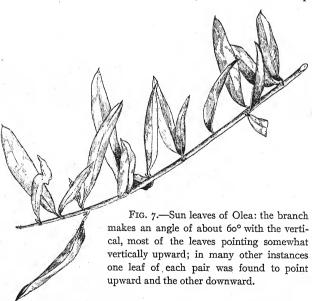
8 For these drawings the author is indebted to Dr. Grace E. Cooley, of Wellesley College.

the transpiration of the sun leaf and the shade leaf would be measured for unequal and rapidly diminishing amounts of contained water. Weighing whole plants growing in sealed pots is out of the question for large shrubs or trees, since seedlings which were small enough to be handled would fail to shade their own leaves and would not



FIG. 6.—Transverse sections of leaves: *A*, sun leaf, and *B*, shade leaf of Olea; *C*, sun leaf, *D*, shade leaf of *Quercus Ilex*. Natural size.

furnish leaves of typical adult form, size, and structure. Weighing leafy twigs with the cut ends immersed in water is not likely to afford the same absolute amounts of loss by transpiration as would be given by the same twigs supplied with water by the normal root pressure



FIG. 7.—Sun leaves of Olea: the branch makes an angle of about 60° with the vertical, most of the leaves pointing somewhat vertically upward; in many other instances one leaf of each pair was found to point upward and the other downward.

of the plant. But the leaves are in a normal atmosphere, and their relative losses (as compared with each other) may be very nearly the same as under absolutely natural conditions.

The plan adopted in the experiments here recorded was to immerse the freshly cut ends of the leafy twigs studied in water contained in

small test tubes. Each stem was carefully sealed into its tube, but a capillary glass tube alongside the stem permitted air to enter to take the place of absorbed water. To show how much of the total loss was due to the cortex, control experiments were made with twigs deprived of their leaves. As it was found that the losses through the cortex sometimes amounted to 15 per cent. of those through the leaves, the plan of covering the entire cortical surface with cacao wax (a mixture of half beeswax and half cacao butter) was finally adopted. Weighings were made on a balance sensitive to less than $5^{mg}$ and the period in most cases allowed for transpiration (two to four hours) usually secured a loss of weight of more than $200^{mg}$ for the least active set of leaves employed. Only sunny days were chosen for the observations, which were all made out of doors. The thermometer ranged, during the season of the experiments and the hours of the day occupied by them, from 18 to 30° (usually from 20° to 25°). Most of the work was done between 12:00 and 5:00 P. M., and the per cent. of relative humidity at 3:00 P. M. was usually under 55. The determination of the per cent. of total illumination under which shade leaves have been developed seems to me an important part of any set of observations on the form, structure, or functional activity of such leaves, and many photometric observations were made on the leaves here discussed. Unless otherwise indicated, the per cents. given are for the illumination at or near midday, at the season stated. In general the shade leaves studied had grown in about the following amounts of illumination: Quercus, 1.5–5 per cent.; Olea, 4–6 per cent.;



FIG. 8.—Sun leaves of Olea: the branch stands nearly vertical and the leaves in general point upward.

Pistacia, 1–4 per cent.; Rhamnus, 4–6 per cent.   The results of the determinations of comparative transpiration are as follows:

| | RATIOS $\frac{\text{LOSS OF SUN LEAVES}}{\text{LOSS OF SHADE LEAVES}}$ | | | |
| | Olea | Pistacia | Q. Ilex | Rhamnus |
|---|---|---|---|---|
| I.  *Sun leaves in sun and shade leaves in shade.* | | | | |
| Maximum........................ | 3.04 | 4.60 | 10.70 | 7.00 |
| Minimum........................ | 1.45 | 2.20 | 1.85 | 2.25 |
| Average of all values obtained....... | 2.10 | 3.70 | 6.35 | 5.91 |
| II.  *Both kinds of leaves in full sunlight.* | | | | |
| Maximum........................ | 2.15 | 2.24 | 3.90 | 1.42 |
| Minimum........................ | 1.17 | 1.00 | 0.96 | 0.52 |
| Average of all values obtained....... | 1.47 | 1.70 | 2.04 | 0.98 |
| III. *Both kinds of leaves in the shade.* | | | | |
| Maximum........................ | 0.97 | 2.58 | 2.70 | 2.61 |
| Minimum........................ | 0.81 | 0.68 | 0.93 | 1.17 |
| Average of all values obtained....... | 0.90 | 1.87 | 1.86 | 1.86 |

Summing up the results of the experiments on comparative transpiration (taking into account some aberrant values not included in the table above given), the following conclusions may be stated:

1. Under the conditions normal for each class (I), sun leaves transpire from three to ten times as much as the shade leaves of the same species.

2. With both classes of leaves under abnormally equal conditions (II and III) the sun leaves of the species studied usually transpire more than one and one-half times as much as the shade leaves.[9]

3. Averaging the averages of II and III, it appears that the inequality of transpiration of sun leaves and shade leaves is about as manifest in sunshine as in the shade.

4. The thinnest and most poorly nourished shade leaves contrast much more sharply with sun leaves in their behavior than do other more normal leaves which have developed in the shade.   This is the principal cause for the difference between maximum and minimum results, particularly noticeable in the transpiration of *Q. Ilex.*

[9] This result is quite at variance with what would probably be the *a priori* opinion of botanists generally, and directly contravenes the statement of WIESNER (Biologie der Pflanzen, 1902, p. 11).

5. Shade leaves exposed for some hours to full sunshine may, without showing any signs of wilting, become almost unable to transpire. For example, a *Q. Ilex* shade leaf that during two hours in sunlight transpired almost one-fourth as much as a sun leaf from the



FIG. 9.—Upper epidermis of Pistacia: *A*, sun leaf; *B*, shade leaf. × 230.

same tree, was afterward in the shade found to transpire about one-sixtieth as much as the sun leaf in the shade.

The fact that shade leaves transpire less than sun leaves, under similar conditions, may at first sight appear singular. But a little consideration will suffice to show that leaves of the former class are structurally unable to perform as much of any kind of work as are
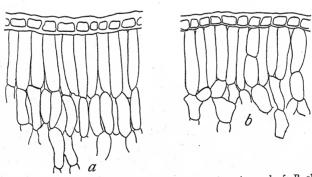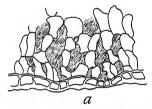


FIG. 10.—Upper epidermis and mesophyll of Pistacia: *A*, sun leaf; *B*, shade leaf. × 125.

the more vigorous sun leaves. The latter, by reason of the much stouter stems from which they spring, and the greater development of the bundles in the leaves themselves, are able to transfer in a peripheral direction larger quantities of water per unit of area per unit of time than shade leaves can. Also sun leaves, with a thickness two to four times that of shade leaves, usually contain much more interior evaporating surface than shade leaves of equal area.

These considerations, however, do not explain all of the observed inequalities of transpiration. Portions of leaves of *Agave americana* freshly cut and with the cut surfaces hermetically sealed with wax, so as to permit no loss of water except through uninjured epidermis, were found to give ratios ranging from 1.5 to 4 for loss of sun leaves compared with that of shade leaves, when both were exposed to full sunlight. Here the transportation of water is an unimportant factor, and the amount of tissue inside the leaf from which the transpired water is drawn was nearly the same in both cases. The Agave shade leaves had grown in a permanent shade of about 2 per cent. illumination.
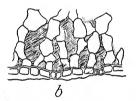


FIG. 11.—Lower epidermis and mesophyll of Pistacia: *A*, sun leaf; *B*, shade leaf. × 125.

It may be of interest to append a statement of the absolute rate of transpiration of the four trees and shrubs discussed in the table above given. The measurements were made with sun leaves a year old, at a temperature of 21° C. and a relative humidity of 67 per cent. The leaves were in moderately bright sunlight.

TRANSPIRATION IN MG. PER 100 $^{sq\,cm}$ LEAF SURFACE PER HOUR.[10]

| | |
|---|---|
| Olea  -      -      -      -      - | 302 |
| Pistacia  -      -      -      - | 231 |
| Q. Ilex      -      -      -      - | 238 |
| Rhamnus      -      -      - | 658 |

These are apparently large values for the transpiration of somewhat xerophytic plants. Leaves of *Ulmus campestris* and of *Pisum sativum* were examined at the same time, for purposes of comparison, and were found to lose 342 and 353$^{mg}$ of water per hour, respectively. This, however, only serves to emphasize a fact too often lost sight of,

[10] Only one surface of each leaf (the lower) is taken into account.

namely that *xerophytic leaf structure is not always incompatible with abundant transpiration, but sometimes exists only for use in emergencies to protect the plant from injurious loss of water.*

In conclusion, the writer can only express his regret that he has so far been able to investigate only one phase of the transpiration of four out of some sixty coriaceous evergreen species which occur in the Mediterranean region. A detailed study of their transpirational activity, month by month throughout the year, could not fail to give results of much value.

NAPLES, ITALY.

# BRIEFER ARTICLES.

## NOTES ON NORTH AMERICAN GRASSES. IV.

### POA FLAVA L. and P. SEROTINA EHRH.

IN the first edition of his *Species Plantarum* (1:68. 1753), LINNAEUS describes this species as follows:

7. Poa panicula diffusa, spiculis ovato oblongis nitidis. Gron. virg. 13.
Gramen pratense majus virginianum. Pet. mus. 239.
Habitat in Virginia.

This has been considered by many authors as identical with *Poa serotina* Ehrh. which occurs in Europe and also in the northern part of North America. The identity of the two was probably assumed from MUNRO's statement: "7. *P. flava*, marked Gron. virg. 13, is *Poa crocata* Michx.; but that name should be altered to *P. flava*." (Identification of the grasses in Linnaeus' herbarium, Proc. Linn. Soc. Bot. 6:43.)

Referring to GRONOVIUS' *Flora Virginica* we find that he cites Clayton 273. Clayton's no. 273, then, becomes the type of *Poa flava* L. Clayton's plants are in the herbarium of the British Museum. Mr. A. B. RENDLE has kindly examined this plant and informs me that it is *Triodia cuprea* Jacq. KUNTZE states that *Poa flava* L., *P. seslerioides* Michx., and *Triodia cuprea* Jacq. are identical, and hence proposes the name *Sieglingia flava* O. K. (Rev. Gen. 2:789). He does not state, however, upon what he bases his statement. The fact that Linnaeus based the name upon a plant collected by Clayton and gave the locality as Virginia should have led American botanists to doubt the reference of *Poa flava* to *Poa serotina*, as the latter plant does not occur in Virginia.

*Poa flava* was taken up by several authors after LINNAEUS, as PERSOON, WILLDENOW, and PURSH, but apparently without knowing the grass, since *Poa seslerioides* Michx. was also retained.

There is still a point upon which more light is needed, that is, the identity of *Poa crocata* Michx. Although MUNRO states that *Poa flava* L. is the same as *Poa crocata* Michx., I cannot confirm this. I did not observe *Poa flava* in Linnaeus' herbarium nor *Poa crocata* in Michaux's herbarium at Paris. From the description and the type locality, near Hudson's Bay, it may well be one of the northern Poas allied to *P. serotina*, such as *P.*

*glauca* Vahl., but can scarcely be *Triodia cuprea* Jacq., which does not occur north of New York. PERSOON (*Syn. Pl.*) refers *P. crocea* [*crocata*] to his *P. hydrophila*, which is given in *Kew Index* as a synonym of *Leersia oryzoides.* Nuttall (*Gen. Pl.*) retains *P. crocata*, and refers to this *P. hydrophila* Pers. as a doubtful synonym.

Furthermore as to the validity of *P. serotina* Ehr. (Beiträge **6**:83. 1791). This rests upon the mention of the name in EHRHART's list of plants entitled "Index Calamarium, Graminum et Tripetaloidearum Linn., quas in usum Botanophilorum collegit et exsiccavit." Miss MARY A. DAY, who has kindly verified the reference for me at the Gray Herbarium, states that the name is mentioned without description, "Poa serotina, Ehrh. Upsaliae." As this is a *nomen nudum*, the name was not technically published, and the next name in chronological order should be taken up. This appears to be *Poa triflora* Gilib. Exerc. Phyt. **2**:531. 1792.

*Poa triflora* Gilib. has been confused in America with *P. nemoralis* L., but both species occur in the northern portions and extend southward in the western mountains. In the northeastern states *Poa triflora* extends southward to Pennsylvania and is quite common northward, while *P. nemoralis* is rare and seems to be introduced.

*P. palustris* L. (*Syst.* ed. 10. 874. 1759) is used by ASCHERSON and GRAEBNER (Synops. Mitteleur. Flora **2**:416) for *P. serotina* Ehrh., but this name is founded on a plate in MORRISON's *History* (p. 201, *pl. 6, fig. 27*), which is *Phalaris arundinacea*, and consequently cannot be used for our plant, *P. triflora* Gilib.

## DIGITARIA Heist.

This is generally cited as "Heist. ex Adans. Pl. Fam. **2**:38. 1763." This is based upon Plukenet, *pl. 190, fig. 2*, which is *Tripsacum dactyloides* L. (*Index* 550). Consequently, according to the recent "Code of Botanical Nomenclature," *Digitaria* Heist. ex Adans. is published (*Canon* 10, 3), and its type is *Coixdactyloides* L. Sp. 972. 1753, inasmuch as LINNAEUS (*l. c.*) cites Plukenet, *pl. 190, fig. 2*. Tripsacum, based upon *Coix dactyloides*, was established in 1759 (*Syst.* ed. 10).

Digitaria as commonly understood was published by SCOPOLI (*Fl. Carn.* 1772). The type of *Digitaria* Scop. is *D. sanguinale*, as this was the first species described. Since the name Digitaria had been used earlier for a different group, certain botanists thought it advisable to reject this name for the group typified by *Panicum sanguinale*, and take up the next name in chronological order, *Syntherisma* Walt.

The fact seems to have been overlooked that the name Digitaria was used at an earlier date than that of ADANSON's *Familles des Plantes.* I

noticed the name in the second edition of FABRICIUS *Enum. Pl. Hort. Helm.* (1763), where it is based upon "Gramen ischaemon Plinii, Clus. H. CCXVII," and "Panicum spicis aggregatis, basi interiore nodosi, flosculis, geminis muticis vaginis foliorum punctatis, L. Sp. 8 ?" Both these citations refer to *Panicum sanguinale* L. This work is at the Missouri Botanical Garden. KUNTZE states that although dated 1763 this work appeared after that of ADANSON. It would appear that the latter author may have adopted the word from FABRICIUS nevertheless. If the name appeared in the first edition of FABRICIUS and with the same type, then there would be no doubt about its antedating ADANSON. I have not been able to find this work in America, but it is in London, and MR. EDMUND BAKER has kindly sent me a transcript of what appears concerning Digitaria. It says "Digitaria Heist. Dactylis Raj. Gramen dactylon majus panicula longa, spicis pluribus nudis crassis. Sloane." (FABRICIUS *Enum. Pl. Hort. Helm.* 207. 1759). The same citation from SLOANE appears under *Panicum dissectum* L. Sp. 57. 1753. Consequently Digitaria is published according to the canon of the code above mentioned.

But *Paspalum* L. was established in the same year (*Syst.* ed. 10. 855, 1759) and is typified by *Panicum dissectum* L., as this is the first species mentioned, although LINNAEUS changes the name to *Paspalum dimidiatum*. There is a curious mix-up here. In the first edition of the *Species Plantarum* LINNAEUS describes as no. 6 *Panicum dissectum*, which is *Paspalum dissectum* L. Sp. ed. 2, to which he erroneously refers Sloane's *pl. 69, fig. 2*, and no. 7, *Panicum dimidiatum*, which is *Stenotaphrum dimidiatum*. In the tenth edition of the *Systema* he publishes Paspalum, but names the first species *P. dimidiatum*, although he bases it upon his *Panicum dissectum* no. 6. SLOANE's plant above mentioned he names *P. virgatum*. In the second edition of the *Species Plantarum* he corrects the difficulty and publishes *Paspalum dissectum* based upon *Panicum dissectum* of the first edition.

There are still two questions to be answered. Which was published first, FABRICIUS or LINNAEUS' *Systema?* Was Digitaria published in some earlier work of HEISTER's?

It may be remarked that HALLER uses Digitaria in the same sense as SCOPOLI and a few years earlier, basing it upon *Panicum sanguinale* and *Cynodon dactylon* (Hall. Stirp. Helv. 2:244. 1768).

The difficulties mentioned emphasize the evil consequences which may arise from changing well known names without sufficient investigation.— A. S. HITCHCOCK, *U. S. Dept. Agriculture, Washington, D. C.*

# OOGENESIS AND FERTILIZATION IN ALBUGO IPOMOEAE-PANDURANAE.

## (WITH TWO FIGURES)

*Albugo Ipomoeae-panduranae* (Schw.) Swingle occurs upon various species of Ipomoea, among others the sweet potato, upon which it inflicts, however, but slight damage. Its most common host is probably *I. pandurata*, in which it induces great hypertrophy of leaves, stems, and flowers. The distortions are so marked as to attract the attention of even the casual observer. It is within these hypertrophied parts that the sexual organs and sexual spores are found in such abundance as to render this species the most favorable of all in the genus for the study of oogenesis and fertilization.

The material is killed in admirable condition if cut in pieces a few millimeters square (the outer part being first shaved off to avoid endangering the knife by adhering sand) and dropped in chrom-acetic acid of the strength recommended for other species of Albugo.[1] The stain chiefly employed is the triple stain of Flemming.

Inasmuch as several other species of Albugo have been described with considerable care, I will detail here only the more salient features, and those which present divergence from the usual types. The early history of oogenesis runs parallel with that of all other species of Albugo investigated; namely, the mycelium enlarges to form the oogonium, the nuclei enter, enlarge greatly, and pass to the spirem condition. This stage presents so little divergence from the same stage in other species that it is adequately represented by *fig. 45* drawn from *A. Bliti*.[2] Following the stage just described comes zonation or the differentiation of ooplasm from periplasm. In various species of Albugo zonation occurs in various ways. In *A. Bliti* the protoplasm condenses in masses which then run together to form the ooplasm.[3] In *A. Ipomoeae-panduranae* zonation partakes more of the character exhibited in *A. candida* and *A. Tragopogonis*, in which the protoplasm may be said to fall away from the oogonial wall, leaving behind only a few strands, sufficient to suspend the oosphere in the center. This type of zonation is sufficiently illustrated by *fig. 27* drawn from *A. Tragopogonis*.[4]

[1] STEVENS, F. L., The compound oosphere of *Albugo Bliti*. BOT. GAZ. **28**:149–176, 225–245. *pls. 11–15*. 1899. (p. 233).

[2] STEVENS, F. L., *loc. cit., pl. 12.*     [3] STEVENS, F. L., *loc. cit., pl. 13, figs. 60–65.*

[4] STEVENS, F. L., Gametogenesis and fertilization in Albugo. BOT. GAZ. **32**:77–98, 157–169, 238–261. *pls. 1–4.* 1901. (*pl. 3*).

With the inception of zonation comes the advance from the spirem to the later stages of mitotic division in all the nuclei of the oogonium. Many of the nuclei in process of division are floated to the periplasm, others complete the division within the ooplasm and there leave both daughter nuclei within the egg. The completion of this mitosis results in conditions very like those in *A. Tragopogonis.*[5] Many of the nuclei are in the periplasm, some are in the ooplasm. The chief difference lies in the coenocentrum, to be discussed later.

The daughter nuclei of the first division, which remain within the ooplasm, proceed to a second mitosis as in *A. Tragopogonis* and *A. candida*, though the number of oospheric nuclei is constantly diminishing, owing to their outward movement. All of them, except one or two contiguous to the coenocentrum, reach the periplasm before or immediately after mitosis is completed. One or two nuclei in mitosis are seen attached to the coenocentrum during the second division. The completion of the mitosis, however, finds only one daughter nucleus remaining thus to function as the female pronucleus. Conclusive evidence was not obtained, but it is probable that some nuclei suffer degeneration within the ooplasm, as is the rule in *A. Tragopogonis*.

The coenocentrum is first to be seen as a homogeneous globule, much like the central globule of *A. Bliti*, though considerably larger, being nearly as large as the nuclei at the completion of the first mitosis. There is no striking differentiation of the protoplasm surrounding the globule at this time. The globule, which does not change materially in size in later periods, is larger than that of *A. Bliti* and much smaller than that of *A. candida*, and it shows much less structural differentiation than is exhibited by the globule in the latter species. When the second mitosis approaches metaphase the globule is surrounded by zones of protoplasm of varying density. In character these resemble the structure shown in *figs. 69* and *71* drawn from *A. Bliti*,[6] though the development attains a higher degree in *A. Ipomoeae-panduranae*.

The attractive power of the coenocentrum for nuclei is evidenced by the attachment of one or more nuclei to it before and during the second mitosis (*figs. 1, 2*), a phenomenon precisely like that already described for *A. Tragopogonis* and *A. candida*. After the completion of the second division the coenocentrum degenerates.

The antheridial tube, shorter in this than in most species of Albugo, opens at about the time of the completion of the second division, emptying

[5] STEVENS, F. L., *loc. cit., pl. 3, fig. 31.*

[6] STEVENS, F. L., The compound oosphere of *Albugo Bliti. loc. cit. pl. 13.*

one male nucleus into the ooplasm. This nucleus joins the female, and each enlarges much before pronuclear union, which is completed in the ruins of the decadent coenocentrum.

Simultaneous with the opening of the antheridial tube begins the construction of the oospore walls. These are completed much as in other species of Albugo, with the exception that there is a slight though very perceptible thickening of the oogonial wall itself. Such thickening is one of the chief features in the spore of Sclerospora, but is not known to occur in any other species of Albugo.



FIG. 1.                              FIG. 2.
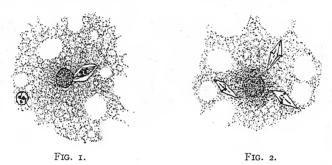
FIG. 1.—Central globule and coenocentrum of *A. Ipomoeae-panduranae* during second mitosis; one nucleus attached.

FIG. 2.—Similar to *fig. 1;* nuclei not yet attached to the coenocentrum.

Subsequent to fertilization, which does not proceed with that extreme slowness noted in some species, the fusion nucleus divides mitotically, increasing the number of nuclei before the assumption of the resting stage.

A minor point, worthy of mention as an indication of chemical composition, is a feature of the staining, conspicuous in this species but not known in any other Albugo. All of that portion of the fertilizing tube which touches the periplasm, and often the whole antheridium as well, takes the gentian-violet with great avidity and retains it longer than do any other structures. Antheridia and antheridial tubes are thus rendered remarkably conspicuous, and dozens are often seen in a single field with the two-thirds objective.—F. L. STEVENS, *A. and M. College, West Raleigh, N. C.*

# CURRENT LITERATURE.

## BOOK REVIEWS.

### Methods of ecological investigation.

ONE OF THE most important recent contributions to the literature of ecology is a work on the development and structure of vegetation, from the hand of Dr. CLEMENTS.[1] The object of this and a forthcoming volume is to present in a systematic and detailed manner the methods of ecological research that have been employed by the author for a number of years in the prairies and woodlands of Nebraska, and in the mountains of Colorado. The principles enunciated here were formulated as working hypotheses in 1898, and have since been submitted to rigorous field tests. The present paper deals in particular with the biological side of vegetation, while the forthcoming work is to be concerned more with the physical aspects.

The fundamental phenomena of vegetation are regarded as invasion and succession (dynamic), zonation and alternation (static), and association, the latter representing the stage to which vegetation has been brought. A section is devoted to each of these topics, and in each case there is given a historical survey of the phenomenon, followed by a keen analysis, and a bibliography. One may classify associations with relation to stratum, light, water, etc., but of these CLEMENTS strongly emphasizes the dominance of the water factor. He inclines not to accept SCHIMPER's edaphic and climatic associations, holding that all but submerged associations are both climatic and edaphic. Invasion consists of the movement (migration) and establishment (ecesis) of species. In discussing this topic, a number of terms are introduced applying to the plant member that migrates, the character of the contrivance which facilitates migration, and the agent involved. Polygenesis (theory of polytopic origin) is carefully analyzed, and the author fully accepts it as a valid theory. Successions are divided into primary (on new soil), and secondary (on denuded soil). Some excellent terms are introduced, indicating the direction of movement in the succession, xerotropic, mesotropic, and hydrotropic, and their application is obvious.

The author gives laws of succession, which will be admitted at once in most cases, though it is likely that some may require modification. Zonation has been more fully considered by former authors than have the other topics treated here, but alternation is a phenomenon that has been discussed and developed only slightly except by Dr. CLEMENTS. Alternation is defined as the response of vege-

[1] CLEMENTS, F. E., The development and structure of vegetation. Botanical Survey of Nebraska. Studies in the Vegetation of the State, III. 8vo. pp. 175. Lincoln. 1904.

tation to the heterogeneity of the earth's surface, and is in sharp contrast to zona-
tion as it is related to topographic asymmetry. A very interesting analysis is
made of competition, which the author holds to be a physical factor in the last
analysis.

This book is most difficult to review adequately, because of the great num-
ber of vital topics which are presented. The presentation is so logical and con-
cise that a satisfactory review or summary would be little less than a verbatim
reproduction of the work. The paper must be digested thoroughly from begin-
ning to end by all who profess to be engaged in ecological research, and it should
be studied by all botanists, especially those who think that ecology may not hope
to deal with facts or have the logic or discipline of other lines of biology.—H. C.
COWLES.

### Leaf ecology.

HANSGIRG, who for a considerable time has been gathering data for such
a work, has issued a somewhat elaborate volume on phyllobiology.[2] The aim
of the author is to present the topic of the biology of the leaf, much as the biology
of the flower has been presented in earlier works. Part I is devoted to a general
consideration of leaf adaptations, especially those adaptations that may be called
protective. Parts II and III make up the body of the volume, and present the
biological classes or types of leaves.

Two general groups are recognized: the water and swamp leaf types of hydro-
phytes and halophytes, and the air leaf types of land plants. The former group
has six subdivisions: the Vallisneria type adapted to currents, the Myriophyllum
type adapted to standing water, the Nymphaea type of floating leaves, the Isoetes
type, the Lysimachia (Naumburgia) type, and the Calla type. More than fifty
types of air leaves are given, among which the following may be noted, so as to
illustrate the method of the author: the violet type of shade leaf, the Trientalis
type (wedge-shaped at base), the Taraxacum type of rosette leaves, the Ipomoea
type of liana leaves, the Cyclamen type (reddish beneath), the Begonia type of
velvety leaves, the Ficus type of gutter-pointed (dripping) leaves, the Populus
type of trembling leaves, the Allium type of tubular leaves, the Phragmites type
of weather-vane leaves, the conifer type of needle leaves, the Eucalyptus type of
profile leaves, the grass type of involute leaves, the Gnaphalium type of hairy
leaves, nyctitropic leaves, the Mesembrianthemum type of thick leaves, the Car-
duus type of spiny leaves, the Drosera type of insectivorous leaves. In each case
there is a detailed description of the leaf type under consideration, together with
a discusion of the ecological advantages of the type. The plants which illustrate
the types are given in considerable detail.

Part III considers the same material, but the arrangement is by plant
families and genera. Part IV considers the protective adaptations of young

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[2] HANSGIRG, A., Phyllobiologie nebst Uebersicht der biologischen Blatttypen von
ein-und-sechzig Siphonogamenfamilien. 8vo. pp. xiv+486. *figs. 40.* Leipzig: Gebrü-
der Borntraeger. 1903. *M*12.

leaves, and twelve types are recognized and discussed. The concluding chapter contains a summary and some concluding remarks.

As might be supposed the author inclines to teleological views, holding that plant structures harmonize with their environment and even tend to become modified in advantageous ways. The volume will have somewhat the function of an encyclopedia, and it is therefore to be regretted that there is no index to genera.—H. C. COWLES.

## MINOR NOTICES.

A REVISED EDITION of COULTER's *Plant Structures*,[3] an elementary text-book of plant morphology, has appeared, the first edition having been published in 1899. There are numerous changes that deal with misstatements, illustrations, changed points of view, and recent discoveries so far as these have to do with the purpose of so elementary a book. Such subjects as mycorhiza, the development of the sporophyte of bryophytes, and the endosperm of angiosperms have been rewritten, and the topic of "double fertilization" introduced.

HELEN EASTMAN[4] has written a fern book for amateurs, which is intended to be "an illustrated field-book that shall be concise, inexpensive, and adapted to the needs of the beginner." The photographs for the plates are said to have been "produced by an entirely original process." The general purpose of such books is to be commended, in so far as they stimulate interest in plants or help to make observation somewhat definite. Doubtless the present book will serve its purpose well in New England.—J. M. C.

ATKINSON[5] has published an outline of his lectures on plant ecology as delivered at Cornell University and they will be of value to all teachers who give ecological courses or who introduce ecological features into general courses. After general lectures on the plant organization, plant organs are considered, then ecological factors, vegetation types, migration. Several lectures on the various formations or societies conclude the series.—H. C. COWLES.

## NOTES FOR STUDENTS.

HITCHCOCK,[6] in a short address on the control of sand dunes in the United States and Europe, gives an account of the European methods of dune control, and makes suggestions for similar work in this country.—H. C. COWLES.

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3 COULTER, JOHN M., Plant Structures. Second edition revised. 12mo. pp. ix+348. *figs. 289*. New York: D. Appleton and Company. 1904.

4 EASTMAN, HELEN, New England ferns and their common allies; an easy method of determining the species. 12mo. pp. xix+161. Boston: Houghton, Mifflin & Co. 1904.

5 ATKINSON, G. F., Relation of plants to environment (or plant ecology). Outlines of course of lectures delivered in the Summer School of Cornell University 1903 and 1904. pp. 67. Ithaca Publishing Co., Ithaca, N. Y.

6 HITCHCOCK, A. S., Controlling sand dunes in the United States and Europe. Nat. Geog. Mag. 1904:43–47.

COSTERUS and SMITH[7] have begun the publication of an account of numerous "monstrosities" observed in the Botanical Gardens of Buitenzorg and elsewhere in the tropics. This is in continuation of a paper published in the same journal in 1895 (p. 97), and deals with monocotyledons. In a subsequent paper dicotyledons and a few cryptogams will be presented.—J. M. C.

POSTGLACIAL fossils have been too much neglected by American paleobotanists. There seems to be no reason why the magnificent results that have been obtained by the Scandinavian investigators should not be duplicated here. PEHR OLSSON-SEFFER[8] has given an account of the methods of bog study (telmatology)employed by Andersson, Sernander, and other Swedish workers.—H. C. COWLES.

SHAW[9] has found that the stamens of Sanguinaria pass the winter in the mother-cell stage; that in Sanguinaria, Chelidonium, and Eschscholtzia there is a stylar canal; that in all three genera the antipodals are very prominent; and that in Sanguinaria and Eschscholtzia the testa is developed from the inner part of the outer integument, while in Chelidonium it is developed from both integuments.—J. M. C.

BOODLE[10] has discovered that a reduced secondary xylem occurs in the stems (both subterranean and aerial) of Psilotum, outside of the solid mass of tracheids described by Bertrand and internal to the ring of sieve tubes. In the lower region of the aerial stem a few cases of apparent mesarch structure were observed. The results strengthen the hypothesis of the affinity of the Psilotaceae with the Sphenophyllales.—J. M. C.

IN A PRESIDENTIAL address before the Linnean Society of New South Wales MAIDEN[11] devotes attention, among other things, to a botanical survey of the country. He suggests a scheme for dividing New South Wales into a number of botanical counties or domains, and gives a list of the most important and accessible papers dealing with each. A plea is made for an ecological study along physiographic lines.—H. C. COWLES.

W. L. BRAY has given an interesting anatomical account of some of the plants of the xerophytic regions of Texas.[12] A study was made of *Agave Lecheguilla*.

[7] COSTERUS, J. C., and SMITH, J. J., Studies in tropical teratology. Ann. Jard. Bot. Buitenzorg II. 4:61–85. *pls. 8–11.* 1904.

[8] OLSSON-SEFFER, P. Examination of organic remains in postglacial deposits. Amer. Nat. 37:785–797. 1903.

[9] SHAW, CHARLES H., Note on the sexual generation and the development of the seed-coats in certain of the Papaveraceae. Bull. Torr. Bot. Club 31:429–433. *pl. 15.* 1904.

[10] BOODLE, L. A., On the occurrence of secondary xylem in Psilotum. Annals of Botany 18:505–517. *pl. 33.* 1904.

[11] MAIDEN, J. H., Presidential address. Proc. Linn. Soc. New South Wales 1902:740–804.

[12] BRAY, W. L., The tissues of some of the plants of the Sotol region. Bull. Torr. Bot. Club 30:621–633. 1903.

*Hesperaloe parviflora, Nolina texana, Ariocarpus fissuratus,* and *Euphorbia antisyphilitica.* The stomatal apparatus, in particular, was found to exhibit marked xerophytic peculiarities. In Ariocarpus there are a number of projections of the cuticular layer into the pit just above the stoma, which virtually makes a series of chambers of the pit.—H. C. Cowles.

CANNON[13] has concluded from anatomical evidence that the two species of mistleto (*Phoradendron villosum* and *P. californicum*) occurring in the vicinity of the Desert Botanical Laboratory (Tucson, Arizona) do not penetrate their hosts by means of solvents secreted by the haustoria; but "the points of admission are determined solely by the character of the host-substratum, whether its cells are loosely put together, as in the lenticels of the cottonwood, or the place where the parasite seeks admission has cellulose cell-walls."—J. M. C.

STAPF[14] has published an account of his studies of the fruit of Melocanna, which is peculiar among grasses in being very large and having a fleshy pericarp. The three species are restricted to India, and the fleshy character of fruit or seed is shared with Melocalamus and Ochlandra. Endosperm is developed only as a delicate parietal tissue, which is soon resorbed by the much enlarging scutellum, the food reserve in the mature fruit being in the fleshy pericarp and the scutellum. Additional facts of interest are that the ovule develops no integuments and that vivipary is an established habit.—J. M. C.

MISS ROBERTSON[15] has studied material of *Torreya californica* from plants cultivated in Great Britain. The microsporangia pass the winter in the mother-cell stage, and the tetrads are formed early in April. No prothallial cell was observed, and during the latter half of May the division resulting in the generative and tube nuclei occurred. Primordia of ovules were observed December 1, and early in April pollination took place. The megaspore mother-cell was not distinguished until late in May, and a month later the reduction division occurred, a linear tetrad being formed. Material did not permit following the development of the female gametophyte and embryo.—J. M. C.

HOLM[16] has been studying the roots of our terrestrial orchids. He finds that a tuberous rhizome is provided only with slender roots, while species with slender rhizomes may possess tuberous roots. The subject is treated under three heads: (1) roots slender, with the leptome and hadrome located in one central cylinder; (2) same, but roots tuberous; (3) roots tuberous, with several cylinders of lep-

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[13] CANNON, W. A., Observations on the germination of *Phoradendron villosum* and *P. californicum.* Bull. Torr. Bot. Club **31**:435–443. 1904.

[14] STAPF, OTTO, On the fruit of *Melocanna bambusoides* Trin., an endospermless, viviparous genus of Bambuseae. Trans. Linn. Soc. London II. Bot. **6**:401–425. *pls. 45–48.* 1904.

[15] ROBERTSON, AGNES, Spore formation in *Torreya californica.* New Phytol. **3**:133–148. *pls. 3–4.* 1904.

[16] HOLM, THEO., The root-structure of North American terrestrial Orchideae. Amer. Jour. Sci. IV. **18**:197–212. 1904.

tome and hadrome. The results show the greatest diversity of structure, even among the most closely allied forms. An interesting observation is that while the roots of our terrestrial orchids form mycorhizas, this is not true of all the roots of the same species, nor of the same individual.—J. M. C.

WESTGATE has been making a study of the reclamation of sand dunes on Cape Cod.[17] The ecological relations of the vegetation are first treated. Ecological factors, mode of sand deposition, development of the range of dunes, natural reclamation, the vegetation of areas which receive gradual accumulations of sand, of areas which receive no such accumulations, and of marshes and bogs are briefly discussed. An account is given of the devastating effects of the dune sand on adjoining areas, and of the means that have been employed to check them. At no other place in this country have artificial plantings in dune sand been carried on so extensively or for so long a time as there.—H. C. COWLES.

BRITTON[18] has made a study of some rather extensive sand plains in the neighborhood of New Haven, Conn., especial attention being paid to the anatomy of the more typical plants. Perhaps the most characteristic species are *Andropogon scoparius* and *Juniperus virginiana*. A fact of much interest is that several species of swamp plants were found on the plains; *e. g., Nyssa sylvatica, Aronia arbutifolia, Vaccinium corymbosum, Kalmia angustifolia, Ilex verticillata, Rosa carolina*. In the anatomical portion of the paper, particular attention is paid to the anatomy of the subterranean organs, a topic that is often superficially treated or even ignored in treatises that are otherwise satisfactory. A number of interesting details are presented, for which recourse must be had to the original.—H. C. COWLES.

STUDIES ON THE PLANT CELL is the title of a series of articles in which DAVIS[19] proposes to describe the chief structures and functions of the plant cell. The subject will be treated under the following heads: (1) structures of the plant cell; (2) the activities of the plant cell; (3) highly specialized plant cells and their peculiarities; (4) cell unions and nuclear fusions; (5) cell activities at critical periods in the ontogeny of plants; (6) comparative morphology and physiology of the plant cell. The opening paper deals with the first of these sections, under the subheads: (1) protoplasmic contents; (2) non-protoplasmic contents, and (3) the cell wall. A list of fifty-five papers is given.

While the subject is in such a condition that critical discussion or philosophical speculation is unsafe, a summary of the literature will be useful to students interested in this subject.—CHARLES J. CHAMBERLAIN.

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[17] WESTGATE, J. M., Reclamation of Cape Cod sand dunes. Bulletin no. 65, Bureau of Plant Industry, U. S. Dept. of Agric. pp. 36. *pls. 6.* 1904.

[18] BRITTON, W. E., Vegetation of the North Haven sand plains. Bull. Torr. Bot. Club **30**:571–620. 1903.

[19] DAVIS, B. M., Studies on the plant cell. Amer. Nat. **38**:367–395. *figs. 1–3.* 1904.

SINCE PARTHENOGENESIS in flowering plants has been proven in only a few genera, it is interesting to note any accessory peculiarities. In parthenogenetic species of Alchemilla, MURBECK[20] finds that the number of chromosomes remains unchanged throughout the entire life history, not showing any reduced number in the gametophytic generation. The behavior of the antipodal nuclei and synergids is also peculiar in Alchemilla, some or all of these five nuclei having the power of motion, so that they behave like polar nuclei. Consequently, it is not at all uncommon to find three or four nuclei at the middle of the sac where one expects to find the two polar nuclei. In such cases the extra nuclei clearly belong to the antipodals or synergids, these regions lacking a corresponding number. Associated with parthenogenesis in Alchemilla is the phenomenon of polyembryony, the extra embryos coming from the synergids or from the cells of the nucellus.— CHARLES J. CHAMBERLAIN.

THE CEYLON PATANAS, which may be compared to our prairies, are forming the subject of an important study by PARKIN and PEARSON.[21] In an earlier paper the junior author gave a general account of the patanas, which are grasslands situated in a region that is otherwise forested. The patanas are of two kinds: wet patanas, located above an altitude of 4500 feet, and dry patanas at a lower altitude. The present paper deals with the anatomical characteristics of their plants, and data have been collected from eighty species. As might be expected, the characters as a whole may be regarded as more or less xerophytic. The most important result is that the plants of the wet patanas are as xerophytic as those of the dry patanas; indeed the former are more hairy, and have a compacter mesophyll. The authors appear to have been surprised at this feature of their results, which, however, seems quite in harmony with the well-known xerophytic characters of the plants of peat bogs and salt marshes.—H. C. COWLES.

WILLE[22] gives the history of the generic name Gloionema, proposed in 1812 by C. A. AGARDH, and, having studied the types in AGARDH's herbarium in Lund, WILLE shows that the specimens on which the genus was founded are eggs of some fly belonging to the Tipulidae. The genus Gloionema, the systematic position of which has been subject to much discussion, has comprised not only these "egg-specimens," but also some diatoms. Since KÜTZING (1849) used the name as a synonym only for certain diatoms, later writers have followed the example. WILLE's object in reviewing the history of this name has been to show the errors and the confusion in nomenclature, which may result from an indiscriminate

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[20] MURBECK, Sv., Ueber Anomalien in Baue des Nucellus und des Embryosackes bei parthenogenetischen Arten der Gattung Alchemilla. Lunds Universitets Årsskrift **38**: no. 2. pp. 11. *pl. 1.* 1902.

[21] PARKIN, J., and PEARSON, H. H. W., The botany of the Ceylon patanas. Jour. Linn. Bot. Soc. **35**:430–463. 1903.

[22] WILLE, N., Ueber die Gattung Gloionema Ag. Eine Nomenclaturstudie. Reprint from "Festschrift zu P. Ascherson's siebzigstem Geburtstage," pp. 439–450 1904.

use of the priority rule and from an imperfect description such as AGARDH'S, which suits not only a great number of different algae within various groups, among them diatoms, red algae, Myxophyceae, and Chlorophyceae, but also insect eggs. He advocates therefore the necessity of furnishing not only a complete diagnosis, but also a good drawing of every new form of thallophytes described. —OLSSON-SEFFER.

MACDOUGAL has published several short papers that will be of interest to the readers of these notes. In a paper entitled "Soil temperatures and vegetation"[23] he gives the results of his thermographic studies, and concludes that too little attention has been paid to soil temperatures; it seems likely that diurnal and seasonal variations, and differences in the temperatures of aerial and subterranean portions must have a large influence on physiological processes, both directly and indirectly. In "Some aspects of desert vegetation"[24] and "Botanical explorations in the Southwest"[25] he gives interesting popular accounts of our deserts and their vegetation, and shows the possibilities of the Desert Laboratory in shedding light on the origin of species. "Mutation in plants"[26] is a sympathetic presentation of the mutation theory, in which the author gives the results of his own cultural studies. The mutants have in all respects the specific characteristics of their Holland prototypes. "Some correlations of leaves"[27] deals with the results obtained in the further development of the shoot and leaf, when resort is had to defoliation. Extra development was awakened in stipules and other organs.—H. C. COWLES.

WILLE and WITTROCK[28] submit to the next International Botanical Congress at Vienna the following propositions: I. In order to establish the right of priority for new species and morphological varieties among the thallophytes, it will be necessary to publish in the future not only a description, but a figure of the organism under consideration, sufficiently clear to make the diagnosis of the species understood. II. In order to maintain the right of priority for new genera among the thallophytes, besides the description there shall also be published (or referred to) a figure of at least one species among those comprising the genus considered. III. These resolutions shall be in force from the first of January 1906. The most beneficial results that would be obtained if these proposals were accepted would be that the identification would be considerably aided by having figures to refer to; such figures would in the future be executed with greater exactness in

[23] Contrib. N. Y. Bot. Gard. no. 44. Mo. Weather Rev. Aug. 1903.

[24] Contrib. N. Y. Bot. Gard. no. 46. Plant World 6:249–257. 1903.

[25] Jour. N. Y. Bot. Gard. 5:89–98. 1904.

[26] Contrib. N. Y. Bot. Gard. no. 48. Amer. Nat. 37:737–770. 1903.

[27] Contrib. N. Y. Bot. Gard. no. 43. Bull. Torr. Bot. Club. 30:503–512. 1903.

[28] WILLE, N., and WITTROCK, V., Motion au Congrès international de Botanique, Deuxième Session, Vienne 1905. Nyt Magasin Naturvidenskaberne 42:217–220. 1904.

order to maintain the right of priority; characters would be more carefully observed, and better diagnoses would be obtained; provisional descriptions, which only tend to confuse the right of priority and are more or less incomplete, would be avoided.—OLSSON-SEFFER.

PRIANISCHNIKOW[29] considers CZAPEK'S conclusion,[30] that no free acid but carbonic is secreted by roots, to be not justified by the experiments. His objections to CZAPEK'S work are, first, that the assertion that aluminum phosphate is insoluble in acetic acid is incorrect; second, that the aluminum phosphate used was not pure, the presence of the hydrate decreasing the solubility; third, that water affected the surface of the gypsum plates used. By using sand mixed with pure iron and aluminum phosphates, the author found that the phosphates were absorbed by the plants, and concluded that root secretions contain organic acids capable of dissolving aluminum and iron phosphates. The solution of phosphates varied with different plants. If it can be proved that carbonic acid secretion varies in consonance with the solution energy of the root system of various plants, and that aluminum and iron phosphates are dissolved by carbonic acid, then there is no need to suppose the presence of other organic acids than carbonic in root secretions. The presence of acid phosphates in the root secretions of seedlings may be explained by the fact that in germination, decomposition of proteid is in excess of synthesis, and the phosphorus set free may be, in part, secreted as phosphates.—L. M. SNOW.

BLACKMAN[31] has discussed the relation of fertilization, apogamy, and parthenogenesis, closely analyzing the processes indicated by these terms. The fact is emphasized that the process of fertilization is almost impossible of definition, in which opinion all biologists will probably concur. In "typical exogamous fertilization," with its fusion of gametes from different individuals, three results at least are apparent: (1) a stimulus to further development; (2) a mingling of two lines of descent; and (3) a doubling of chromosomes. Starting with this primitive type, a series of reduced processes is indicated in which one or more of these characteristic results of fertilization have been lost. For example, "self-fertilization," common among angiosperms, no longer brings about the mingling of different hereditary properties; and cases of apogamy preceded by nuclear fusion is a still more reduced form of fertilization in the same direction. Many of the so-called cases of parthenogenesis are regarded as still further cases of reduction of the primitive process, for there has not even been the formation of a potential egg, in the sense that there has been a reduction division. In this sense, it is claimed that true parthenogenesis has not been proved among the higher plants. Since there is no reduction division, there is no true gamete, and the

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[29] PRIANISCHNIKOW, D., Zur Frage über die Wurzelausscheidungen. Ber. Deutsch. Bot. Gesells. **22**:189–190. *pl. 12.* 1904.

[30] CZAPEK, Jahrb. Wiss. Bot. ————————. 1896.

[31] BLACKMAN, VERNON H., On the relation of fertilization, "apogamy," and "parthenogenesis." New Phytol. **3**:149–158. 1904.

resulting embryo is really a case of sporophytic (somatic) budding. In such cases the reduction of the primitive process of exogamous fertilization is complete; the mingling of different characters, the stimulus to development, and the doubling of chromosomes all having disappeared.—J. M. C.

BRAY[32] finds that according to their character and distribution the forests of Texas are to be classified as the east Texas timber belt, the timbered area of Edwards plateau, the live oak timber belt, the Rio Grande plain chaparral, the mesquite, and the timber of the Cordilleran region. According to the habitat of its different components, the eastern timber belt is subdivided into the following types: the swamp and bayou forests, the hardwood forests of the alluvial bottoms, the mixed hardwood forest of the interior of the coast plain, the long-leaf forests of the Fayette prairie, and the hardwood and short-leaf forests of the lignitic belt. Under each of these headings follows a brief but very careful analysis of the factors determining the present condition of the tree growth in each forest type. From the economic standpoint the bulletin shows that only 10 per cent. of the entire area of Texas is covered with a merchantable forest; 125,000 acres, yielding nearly a billion feet of lumber, are being cut over annually. The timber is cut in such a way that the land does not reproduce valuable forests. The author gives valuable and timely suggestions in regard to forest management both for private owners and for the state.

The same author[33] has studied the forests of the Edwards plateau with special reference to their relation to the water supply. The plateau is composed of limestone, and the naturally high water-absorbing capacity of the rock is enhanced by the position of the strata and by the numerous extensive fissures and caverns. Thus the region forms a vast catchment area for the water which supplies the agricultural lands below. The rapid collection and run-off of the waters from the bare slopes cause frequent disastrous floods. The writer shows how covering the slopes with tree growth (which is rapidly taking place naturally) tends to reduce both the frequence and the eroding power of the floods. By conserving the waters of the plateau in this manner they could be used to irrigate the rich but arid lands of adjacent plains. State ownership for this purpose is recommended.

These two bulletins are valuable contributions to our knowledge of the life-relations of trees, and they demonstrate the value of careful ecological study in dealing with certain problems of practical forestry.—CLIFTON D. HOWE

ITEMS OF TAXONOMIC INTEREST ARE AS FOLLOWS: CARL MEZ (Bull. Herb. Boiss. II. 4:619–634. 1904) has published new species of Bromeliaceae in Greigia, Aechmea (2), Billbergia, Pitcairnia (9), and Puya (7).—O. VON SEEMEN (idem

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[32] BRAY, WILLIAM L., Forest resources of Texas. U. S. Dept. Agric., Bureau of Forestry. Bull. no. 47. 1904.

[33] BRAY, WILLIAM L., The timber of the Edwards plateau of Texas; its relation to climate, water supply, and soil. U. S. Dept. Agric., Bureau of Forestry. Bull. no. 49, 1904.

651–656) has published two new species of Quercus from Costa Rica.—A. THEI-LUNG (*idem* 695–716), in the first of a series of studies of Lepidium, has replaced the *L. virginicum* of American authors by *L. densiflorum* Schrad., has disentangled from the same confused mass of forms the new species *L. neglectum*, and has described a new related species (*L. costaricense*) from Costa Rica.—C. A. M. LINDMAN (Arkiv for Botanik **1**:7–56. 1904) has published a critical review of the American species of Trichomanes, based on collections in Swedish herbaria and on specimens obtained by the author in Brazil, 3 new species being described; and has also (*idem* 187–276) published an account of a collection of Brazilian ferns containing 16 new species.—M. L. FERNALD (Rhodora **6**:162. 1904) has published a new species of Alnus (*A. mollis*) from Canada and adjacent Eastern United States.—E. P. BICKNELL (Bull. Torr. Bot. Club **31**:379–391. 1904), in presenting the Californian species of Sisyrinchium, has described 5 new species.— P. A. RYDBERG (*idem* 399–410), in his 11th "Studies on the Rocky Mountain flora," has described new species of Juncus (3), Juncoides, Allium (2), Corallorhiza Salix, Atriplex (2), Corispermum, Claytonia, Cerastium, Arenaria (3), Alsinopsis, Lychnis, Stanleya, and Schoenocrambe.—N. PATOUILLARD (Bull. Soc. Mycol. France **20**:136. *fig. 1.* 1904) has described a new genus (*Seuratia*) of Capnodiaceae on the leaves of the coffee plant.—H. HARMS (Ann. Jard. Bot. Buitenzorg II. **4**:13–16. 1904) has described a new East Indian genus (*Anomopanax*) of Aralia-ceae, comprising 3 species.—S. H. KOORDERS (*idem* 19–32. *pls. 2–3*) has described a new genus (*Teijsmanniodendron*) of Verbenaceae under cultivation, its nativity being unknown.—G. R. SHAW (Gard. Chron. III. **36** : 122. *fig. 49.* 1904) has described a new pine (*P. Nelsoni*) from northeastern Mexico.—W. A. MURRILL (Bull. Torr. Bot. Club **31**:415–428. 1904), in his eighth paper on the Polyporaceae of North America, has presented Hapalopilus and Pycnoporus, and described 6 new monotypic genera (*Abortiporus, Cyclomycetella, Cycloporus, Globifomes, Nigro-fomes,* and *Poronidulus*).—N. L. BRITTON (Torreya **4**:124. 1904) has described a new species of Alnus from New York.—J. M. C.

BLAKESLEE has published in full[34] the results of his studies upon the sexual reproduction in the Mucorineae first announced in *Science* June 3, 1904. This brilliant work has completely revolutionized our views of the condi-tions that influence the production of zygospores. While most investigators have been trying to determine external factors such as increased humidity, high temperature, seasonal conditions, etc., as the stimuli to zygospore formation, BLAKESLEE finds that it "is conditioned primarily by the inherent nature of the individual species and only secondarily by external factors."

BLAKESLEE shows that the Mucorineae fall into two groups. The first, termed the homothallic group, comprise "the minority of species (ex. Sporodinia) and form their zygospores from branches of the same thallus or mycelium, and can be obtained from the sowing of a single spore." The second group, termed

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[34] BLAKESLEE, A. F., Sexual reproduction in the Mucorineae. Proc. Am. Acad. **40**: 205–319. *pls. 4.* 1904.

heterothallic, contains a large majority of the species (ex. Rhizopus, Mucor, Phycomyces), each of which is made up of two sexual strains, so that the "zygospores are developed from branches which necessarily belong to thalli or mycelia diverse in character and can never be obtained from the sowing of a single spore. . . . . Every heterothallic species is, therefore, an aggregate of two distinct strains, through the interaction of which zygospore production is brought about."

These sexual strains show in general a greater or less vegetative luxuriance and are designated by the + and − signs respectively. ·The two strains only form zygospores when growing together, as the progametes "arise from the stimulus of contact between the more or less differentiated hyphae (zygophores) and are from the outset always normally adherent."

"A process of imperfect hybridization will occur between unlike strains of different heterothallic species in the same or even in different genera," *i. e.*, the gametes are formed by the chemotactic stimulus of contact with the mycelium of an opposite strain. This peculiarity makes it possible to determine the strain of an unknown form by cultivation with the strains of determined material and is most interesting as evidence that the stimulus to zygospore formation is chemical rather than the rougher physical conditions. These attempts at hybridization were not observed to go farther than the cutting off of the two gametes.

BLAKESLEE concludes from his studies: (*a*) that the formation of zygospores is a sexual process; (*b*) that the mycelium of a homothallic species is bisexual; (*c*) that the mycelium of a heterothallic species is unisexual; and further (*d*) that in the + and − series of the heterothallic group the two sexes are represented.— B. M. DAVIS.

THE CONDITIONS influencing the production of zoospores in Chlamydomonas have been studied by FRANK,[35] who shows that a decrease in concentration of Knop's solution acts as a stimulus, as does also, but in a secondary way, decrease in light intensity. Temperature limits were also studied, with the conclusion that this factor is only a secondary one in the production of zoospores. The alga bears concentrations up to 2.5 per cent. Knop's solution. In the higher concentrations the cells are larger and their contents more dense. On solid substrata soaked with solution the plant behaves much as in a more concentrated solution. The transfer of cells from Knop's solution to solutions of various single chemical salts influences the production of zoospores variously according to the salt used. Thus, as has been shown before, K is somewhat more poisonous than Na. With all the salts used a concentration is soon obtained wherein no zoospores are produced. The osmotic pressure of the solution at this concentration-limit sometimes lies above, sometimes below, and sometimes is equal to that of the limiting concentration for Knop's solution. From this the author concludes that the stimulus producing zoospores is not an osmotic one when the mere reduction of concentration in the nutrient medium is involved. I cannot

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35 FRANK, THEODOR, Cultur und chemische Reizerscheinungen der *Chlamydomonas tingens*. Bot. Zeit. **62**[1]:153–188. *pl. 6.* 1904.

see how this follows, for in all the simple solutions used there was a lack of the other salts normally present in the Knop's solution. Thus, in the study of these poisons more than one factor has been varied. The strengths of solution used are throughout stated in percentages, and the obsolete method of isotonic coefficients is used in calculating osmotic pressures, so that it will be necessary to transform the data to more modern terminology before they can be of wide use in comparison. The methods and terminology of physical chemistry are most suitable for this sort of investigation. The general results of this part of the paper are as follows: Production of new motile cells can take place only with a reduction of the concentration of the medium. The process is checked by the presence of many substances, and these act chemically rather than osmotically, *i. e.*, they act like poisons.

The zoospores of this alga are positively phototactic towards blue light of not too great intensity, but after a limiting intensity is passed they are negatively so. They are sensitive to very weak light. It would be well if such observations as these could be made with a photometer, such as a silver salt perhaps, so that limits of light intensity might be definitely stated. The chemotactic responses of these same cells were also investigated, as were also those of *Euglena gracilis*, but the results cannot be stated here.—B. E. LIVINGSTON.

THE EXPERIMENTAL morphology of *Achlya polyandra* has been studied, albeit in a somewhat medieval way, by HORN,[36] working in KLEBS's laboratory at Halle. He shows that the presence of metals in the nutrient medium, as well as of traces of metallic salts, has a marked effect on both vegetative and reproductive activity of this organism. In such media the hyphae, which are normally without cross walls, develop such walls, often at regular intervals, and the filament often becomes divided up into polyhedral chambers, like irregular parenchyma, by walls in all directions. The same effect is brought about by partially plasmolyzing healthy hyphae and then returning them to the normal medium. But there appears to be a difference in the nature of the cross walls in these two cases; those produced by a metal are not doubly refractive and consist largely of pectin, while those produced by plasmolysis are anisotropic and contain much cellulose. However, the latter form of walls is at first exactly like the former; the difference appears later. The general response of the plant is quite parallel to that which I have obtained in Stigeoclonium,[37] the formation of cross walls

[36] HORN, L., Experimentelle Entwicklungsänderungen bei *Achlya polyandra* de Bary. Ann. Mycol. **2**:207–241. *figs. 21*. 1904.

[37] For the effect of external osmotic pressure upon Stigeoclonium see LIVINGSTON, B. E., On the nature of the stimulus which causes the change of form in polymorphic green algae. BOT. GAZ. **30**:361–377. *pl. 22*. 1900. Also, Further notes on the physiology of polymorphism in green algae, *ibid.* **32**:292–302. 1901. The recent work on the effect of metallic salts upon this same plant was reported in part at the St. Louis meeting of the Am. Ass. Adv. Sci., Dec. 1903. See Science N. S. **19**:173. 1904. The fuller discussion of this subject is about to be published in the Bull. N. Y. Bot. Garden.

and of irregular division being quite parallel to the production of the palmella form in my alga, which is brought about by many metal salts as well as by high osmotic pressure of the medium. Perhaps if HORN's poisoned material had been transferred to a normal medium at an early stage in the development of cross walls the same cellulose formation would have occurred as that which he observed in the partially plasmolyzed filament.

Regarding the production of zoospores, the unsatisfactory and almost meaningless general observation is made again, as it has been made with other forms, that these bodies are produced "when a sufficient amount of nutrient material for growth is no longer present in the medium." This is of course not exact science. They are produced at a temperature of from 5° to 31° C. "Osmotic pressure has only an indirect effect." Intercalary sporangia are produced in the filaments poisoned with metal and also in those which have been partially plasmolyzed for a short time; indeed, all the cells of the parenchyma-like masses above described seem to be potential sporangia. This last observation seems to agree quite accurately with that made in the case of Stigeoclonium, that palmella cells are capable of producing zoospores when in weak media, whether the plant has been brought to this form by metallic poison or by external osmotic pressure.

These are the main results of the paper. It is to be regretted that good experimentation should be brought to so little account by such vagueness of thought as indicated in the adoption of NÄGELI's theory of the oligodynamic effect of metals, which has no real basis in experiment, and the idea that nutrition is somehow a thing apart from chemical stimulation and response. The present paper appears to "strike only the high places," as the phrase goes. What is needed in physiological work is more of the methods of the physical chemist.—B. E. LIVINGSTON.

LAWSON[38] has published the results of his investigation of *Cryptomeria japonica*, concerning which we have had heretofore only ARNOLDI's somewhat meager account. The material was obtained chiefly from trees growing on the campus of Stanford University. The staminate cones appear early in October, the reduction division occurs the first week of November, and by December the microspores are rounded off. In January the first nuclear division takes place, resulting in generative and tube nuclei, no prothallial cell being formed. Pollination occurs during the latter part of February, and the pollen tubes, without branching, advance directly towards the embryo sac. The generative nucleus divides early in the pollen tube development, and the body cell becomes very large, consorting with the tube- and stalk-cell nuclei in the tip of the tube. About the middle of June the male cells are formed and fertilization occurs.

Deep in the nucellus three or four mother-cells become differentiated early in March, each giving rise to a tetrad. The centrally placed megaspore of the twelve to sixteen potential ones functions, the development of the female gamet-

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[38] LAWSON, A. A., The gametophyte, fertilization, and embryo of *Cryptomeria japonica*. Annals of Botany **18**: 417–444. *pls. 27–30*. 1904.

ophyte proceeding as usual, so far as parietal placing and centripetal growth are concerned. The method of forming the permanent endosperm tissue is remarkable, and is either unusual among gymnosperms or has escaped observation. The primary endosperm cells, that is those open towards the center of the sac, elongate inward, and free nuclear division proceeding they become multinucleate. Then comes a stage when "hundreds of the free nuclei divide about the same time," but no cell plate is formed between the daughter nuclei, the kinoplasmic fibrils extending between them increasing in number and curving outwards on all sides until both nuclei are completely surrounded by a sheath of fibrils which fuse, thus forming an investing membrane. This method of free cell formation goes on throughout the whole of the prothallium except in the region of the archegonium initials, the cells becoming crowded and thus resembling ordinary tissue composed of binucleate cells. After this tissue has been organized nuclear division with cell plates proceeds in the usual way.

The archegonium initials were observed about May 25, and eight to fifteen archegonia are organized into a complex invested by a common layer of jacket cells. The neck cells are usually four in number, and just before fertilization the nucleus of the central cell divides into ventral canal and egg nuclei, without the formation of any separating membrane. Only one male cell enters an egg, two eggs thus being fertilized from one tube, and the male nucleus is liberated from its cytoplasmic sheath only after the male cell has become imbedded in the egg cytoplasm.

The proembryo begins with the formation of four free nuclei, in one case six being observed, which pass to the base of the egg and begin the divisions that result in the two tiers of cells and four free nuclei. The cells of the upper tier elongate to form the long and tortuous suspensor, and one or several embryos may be developed from a single egg. The estimated but not definitely counted number of chromosomes was nine or ten for the gametophyte and eighteen or twenty for the sporophyte.

The general conclusion is reached that the structures of Cryptomeria are distinctly of the Cupresseae type.—J. M. C.

# NEWS.

Dr. J. P. Lotsy has been appointed reader in botany in the University of Leiden.

Dr. W. A. Murrill has been appointed assistant curator at the New York Botanical Garden.

Professor G. Bonnier has been elected an honorary member of the Royal Microscopical Society of London.

Dr. K. Linsbauer has become *privat-docent* for anatomy and physiology of plants in the University of Vienna.

Professor P. A. Saccardo has been elected a corresponding member of the Reale Accademia dei Lincei of Rome.

B. M. Everhart, known best through work in systematic mycology done in association with Mr. J. B. Ellis, died at West Chester, Pa., on September 22, at the age of eighty-seven years.

The Imperial Academy of Sciences at Vienna granted 4,000 kroner to Hofrat Professor Julius Wiesner for his journey to the Yellowstone National Park, where he expected to study the light relations of the flora. Unfortunately illness seriously interfered with his plans, and he had not fully recovered at the time of the Congress at St. Louis. Professsor Wiesner delivered his address, however, in spite of evident weakness.

Thomas H. Kearney, of the Bureau of Plant Industry, United States Department of Agriculture, has been authorized to proceed to North Africa and other Mediterranean coast regions for the purpose of securing new seeds and plants adapted to the southwest. A special study will be made of the date, and new introductions of this fruit will be undertaken. Alkali-resistant forage crops will also be studied and the introduction of seeds of new and promising kinds will be made. Mr. Kearney will remain abroad until next spring.—*Science.*

A section of biogeography was organized in connection with the Eighth International Geographic Congress, which met in Washington, September 8–10. Professors Heilprin and Harshberger, both of Philadelphia, acted respectively as chairman and secretary. The papers of botanical interest were as follows: Oscar Drude, *Die Methode der pflanzengeographischen Kartographie, erläutert an der Flora von Sachsen,* and *Nomenklatur pflanzengeographische Formationen;* J. W. Harshberger, *Method of determining the age of the different floristic elements in the eastern United States;* Charles C. Adams, *The dispersal centers of North American biota;* H. C. Cowles, *The remarkable colony of northern plants along the Apalachicola River, Florida, and its significance;* David White, *The*

*American range of the Cycadofilices.* A paper entitled *The importance of the physiographic standpoint in plant geography*, by H. C. Cowles, was read by title. It was greatly regretted that Prof. Flahault, who was to have read a paper entitled *La cartographie de géographie botanique*, was detained in France by illness. The biogeographical sessions were well attended, although there were few visiting botanists present, and the papers excited lively discussions.

The International Congress of Arts and Science held at St. Louis, September 19–26, secured the attendance of large numbers of scientific men, both American and foreign. It is safe to say that no more distinguished body of scholars has ever been gathered on this continent, or probably on any other. The formal addresses by botanists were as follows: John Merle Coulter, University of Chicago, *Development of morphological conceptions;* Hugo de Vries, University of Amsterdam, *Fundamental conceptions of evolution;* Frederick O. Bower, University of Glasgow, *The relation of the axis to the leaf in vascular plants;* Karl F. Goebel, University of Munich, *Die Grundprobleme der heutigen Pflanzenmorphologie;* Julius Wiesner, University of Vienna, *Die Entwickelung der Pflanzenphysiologie unter dem Einflusse anderer Wissenschaften;* Benjamin M. Duggar, University of Missouri, *Present problems of plant physiology;* Joseph C. Arthur, Purdue University, *The history and scope of plant pathology;* Merton B. Waite, U. S. Department of Agriculture, *Vegetable pathology as an economic science;* Oskar Drude, Royal Technical College, Dresden, *Die Stellung der Oekologie in der heutigen Wissenschaft;* Benjamin L. Robinson, Harvard University, *Problems in ecology.* These addresses will be published in the volumes of *Proceedings* of the Congress. Short (ten-minute) papers were read by J. M. Coulter, *Morphology of Torreya taxifolia;* J. A. Harris, *The importance of the investigation of seedling stages;* C. E. Bessey, *Distribution of trees in Nebraska.*

The marine station of the University of Washington has completed a successful summer's work among the San Juan islands in the northern part of Puget Sound. The object of the work was to determine the marine life of the Sound among the islands, and to begin the study of the distribution of species on the sea bottom from the ecological point of view. The station was in charge of Professor Trevor Kincaid (zoology) and Dr. T. C. Frye (botany). The party included the majority of the teachers of biology in the colleges, normal schools, and large high schools of the state, as well as a number from adjacent ones. Headquarters were established at Friday Harbor, where house room was secured for laboratories, storeroom, etc., while the party lived in tents pitched in the dense coniferous forests on the shore. The party had at its disposal a naphtha launch, and a scow fitted with wire cable, windlass, dredges, and nets, by means of which the bottom in the straits and inlets among the islands was pretty well explored. Carrying their camping utensils with them in the launch, the party was enabled to make trips from headquarters extending over several days and thus cover a large area. Large collections were made of algae, shells, and hydroids, and valuable data were secured concerning their distribution. Professor Cutting, of the State

University of Iowa, took charge of the hydroids collected. The University of Washington is endeavoring to locate the richest field in the Sound for the purpose of establishing a permanent marine station. The site has not yet been definitely located, but it is expected that one will be determined upon before spring.

THE MEETING of the British Association for the Advancement of Science, held this year at Cambridge, August 17–24, was attended by an unusually large number of British botanists and by many foreign botanists as guests.

The president of the botanical section, FRANCIS DARWIN, discussed, critically and sympathetically, the hydrostatic and the statolith theories regarding the perception of gravity by plants, expressing the conviction that, at the present time at least, the latter theory has most in its favor, but admitting that it is not yet proved. About sixty papers were presented, representing the whole field of botanical study. A group of papers on paleobotany showed the extent and the fruitfulness of this line of investigation in England. Many of these papers were illustrated by lantern slides, often of great beauty, and always interesting. The group of papers by the ecologists showed by the careful anatomical and experimental investigations, coupled with examinations of soil, drainage, and meteorological conditions, that the thoroughness and accuracy which alone can give ecology any real value are recognized and applied in England and Scotland. There were also papers on mycology, morphology and cytology, anatomy, and physiology. One of the pleasantest features of this meeting was the dinner of the botanists, about seventy, in St. John's College. The speeches by DARWIN, ENGLER, CHODAT, FUJII, SEWARD, and WAGER were felicitous, and the cordial reception accorded to FUJII, of Tokyo, was especially interesting at this time. As one of the guests of the Association, I cannot refrain from expressing my grateful appreciation of the gracious courtesy and hospitality which were extended to all.—G. J. PEIRCE.

# BOTANICAL GAZETTE

## *NOVEMBER, 1904*

### A FOSSIL SEQUOIA FROM THE SIERRA NEVADA.[1]

#### EDWARD C. JEFFREY.

#### (WITH PLATES XVIII AND XIX)

AMONG the material of fossil woods stored in the basement of the Botanical Museum of Harvard University is a large piece from the line of the Central Pacific Railway. It is catalogued as no. 7354 and is described on the label as "From tunnel no. 1, Central Pacific R. R., Blue Gap, Sierra Nevada Mountains. Elevation above the sea 4520 [ft]. Found under 60 [ft] of conglomerate." There is no further information as to the time of its collection or the formation from which it was derived. As the piece of wood in question had the color and general texture of a Sequoia, I was led to investigate its microscopic structure, with the result that it turned out to be a new species of the genus, presenting a number of interesting and novel features.

Dr. F. H. KNOWLTON, of the United States Geological Survey, has expressed the opinion that the wood which forms the subject of the present article is of the age of the auriferous gravels, *i. e.,* Miocene; but is unable to state positively that this is the case, on account of the absence of definite evidence. As the location of the specimen is clearly indicated, it will probably be an easy matter to determine subsequently its exact geological horizon. In any case the morphological features which it presents are of sufficient interest to justify a description at the present time.

The fragment of wood in its original condition as taken from the collection was about 1.5[m] long. One end was much frayed and

[1] *Contributions from the Phanerogamic Laboratories of Harvard University.* No. 1.

water-worn; the other showed a fractured surface as if it had been broken away from a longer piece. This supposition is strengthened by the fact that there are a few ax marks on the broken end of the specimen. The piece measured about $15^{cm}$ in the radial direction and about $18^{cm}$ tangentially, and is rounded in these directions apparently by water carriage. There are about three hundred rings of growth, and perpendiculars drawn from these show that the original trunk of which the specimen under discussion is a fragment must have been at least six feet in diameter. It was possibly much larger, since in all probability a good deal of ligneous tissue has disappeared from the outer surface of the specimen. The wood had undergone comparatively little alteration from decay, and the fact that it is only very slightly impregnated with silica, easily removed with hydro-fluoric acid, makes it very favorable for investigation. The preservation even of minute details of structure is far beyond that of any other fossil Sequoia with which I am familiar.

*Fig. 1* shows some of the characteristic features of a transverse section of the fossil wood under discussion. The annual rings are well marked and very regular even in sections of greater area than that shown in the figure. Two peculiarities stand out above all others in *fig. 1*, viz., the apparent absence of resin cells, such as ordinarily occur in cupressineous woods, and the presence of resin canals in both horizontal and vertical planes, a feature characteristic of the Abietineae and hitherto unknown in the cupressineous series. The rings of growth are mostly composed of thin-walled tracheids, but suddenly toward the outer border of the annual zone appear a few thick-walled tangentially flattened elements. In one of the annual rings may be seen a number of open spaces rounded in outline. These are vertical resin canals in transverse section, and are confined to the spring wood. A very broad horizontal duct originates outwardly from the vertical series of resin canals just described and passes beyond the boundary of the figure. *Fig. 2* shows some thin annual rings highly magnified. The tracheids are more often square than pentagonal or hexagonal in outline. The pits are confined to their radial walls, except in the case of the thick-walled autumnal tracheids, and are obviously in two rows as seen in transverse section. The tangential pits which are sometimes found in the spring wood of the

living Sequoias are not found in the present species.[2]   On the left of
the figure may be seen a medullary ray.   The cells are obviously very
long, and in the present instance extend across a complete annual
ring.   The elements still retain their dark granular contents, the
so-called resin globules.   In the present species of Sequoia the
resinous material is mainly found in the medullary rays and scarcely
at all in the wood, in this respect presenting a marked resemblance to
Tsuga and Abies among the Abietineae.   There is, however, a cer-
tain number of resin cells on the outer face of the summer wood.
One of these elements is shown in the second annual ring and on the
right of the figure.   This feature, too, finds a parallel in Tsuga among
the Abietineae.

   *Fig. 3* shows part of a tangential section of the wood of our
species, under low magnification.   The irregular dark striping of
the center of the figure represents the summer wood, while the light-
colored lateral portions correspond to the spring wood.   Most of the
medullary rays appearing in the figure are so small as to be scarcely
discernible, but some of them are enormously enlarged to constitute
fusiform rays, which contain horizontal resin canals.   Most of these
canals appear to be empty, but some are obviously filled with coarsely
granular contents.   The appearance presented in the section shown
in our *fig. 3* is somewhat exceptional for the species under discussion.
In most cases a tangential section of the wood reveals no fusiform
rays and no horizontal resin canals.

   *Fig. 4* appears to afford an explanation of the peculiarities seen
in *fig. 3*.   The magnification in this instance is not great, and as a
consequence a large number of annual rings are present.   These
become arched and suffer interruption toward the lower part of
the figure.   In this case we have obviously to do with a healing
wound.   The interruption in the continuity of the annual rings
indicates the time at which the injury took place, and outside this
gap the rings of growth are unusually thick, as is ordinarily the case
in traumatic wood.   There is a reaction farther out and the rings
become much thinner, again to increase their thickness once more
still farther out.   From the right border of the wound a horizontal

   [2] PENHALLOW, D. P., Generic characters of North American Taxaceae and
Coniferae.   Trans. Roy. Soc. Canada **2**:1896.

resin canal can be seen making its way outward through all the annual rings seen in the plane of the figure.   By careful inspection it is also possible to make out that there are vertical canals in series in the spring wood of the first ring of ligneous growth subsequent to injury.   *Fig. 5* shows part of another section through the same wound more highly magnified.   The tangential series of resin canals in the spring growth of the first traumatic ring can now be clearly seen.   Passing off from these can be made out three horizontal ducts, the most median of which does not actually communicate with the vertical canals in the plane of the present section.   To the right of the figure a short tangential series of ducts can be seen in the second ring of growth formed after the wound.   No horizontal canals originate from this weaker series of vertical canals.   *Fig. 6* is taken from the center of the wounded region, and the annual rings immediately abutting on the wound are the second and third formed subsequent to the injury.   Each of them contains a weak series of vertical canals in the vernal wood, but these do not give rise to any horizontal ducts.   *Fig. 7* shows a part of another section through the same wound, somewhat more highly magnified.   The vertical canals of the spring wood are now clearly discernible, and from these are passing off in the horizontal direction three huge resin canals. Two of these are more or less completely filled by parenchymatous tyloses.

We are now in the position to discuss the resin canals vertical and horizontal appearing in *figs. 1* and *3*.   It is a well-known fact that in the Abietineae the formation of resin canals may be brought about as the result of wounds.   The present writer has shown that the same feature is found in the living species of Sequoia.[3]   In the existing species of Sequoia the formation of traumatic resin canals is entirely confined to the vertical plane, so far as our present knowledge goes.   In those Abietineae which give rise to ligneous resin canals only as a result of injury they are also confined to the vertical plane, except in the genus Cedrus, where, as the present author shows in an article about to be published, they are formed horizontally as well.   Three cases of injury have been found in the fossil Sequoia at present under consideration, and in each of the three cases the injuries led to the

3 JEFFREY, E. C., Memoirs of the Boston Society of Natural History 5: no. 10.

formation of traumatic resin canals. Where the irritation is most severe, *i. e.*, in the first annual ring formed after injury, there are apt to be both horizontal and vertical canals; while in the later formed rings the impulse gradually dies out and only vertical canals originate. The horizontal canals run in considerable numbers from the margins of healing wounds. *Fig. 3* represents a section through such a patch of traumatic horizontal canals. *Fig. 8* shows the appearance of the large horizontal canal to be seen on the left of *fig. 3* when somewhat more highly magnified. The enormously enlarged medullary ray is almost entirely taken up by the huge resin canal, which in turn is occluded by a mass of cells constituting a tylosis. *Fig. 9* shows a smaller duct from the right of *fig. 3* somewhat more highly magnified than the foregoing. The continuity between the tylosis and the wall of the duct can clearly be made out in this figure. The cells constituting the walls of the traumatic resin canals in the Sequoias are thick-walled and much pitted, and generally contain in greater or less abundance the dark brown masses which occur in the resin cells of the wood of the Cupressineae in the larger sense. Not all of the canals contain tyloses in the fossilized material, but it is probable that they were universally present in the living tree.

*Fig. 10* shows the transition from a vertical to a horizontal duct as seen in vertical radial section. The great difference in size which ordinarily obtains between the two sorts of ducts is very apparent. The abundant tyloses are also a feature of the horizontal ducts, although this phenomenon is also occasionally found in the vertical resin canals.

Vertical traumatic resin canals may extend very far above and below the wound, so that in small isolated pieces of wood their relation to injury is not obvious. From a wide knowledge of living forms of conifers in relation to injury, I am in the position to state inductively that rows of vertical ducts occurring vertically and tangentially in coniferous woods are always due to injury. It has been possible to show that this is the case wherever the material was abundant enough to warrant a definite conclusion.

Horizontal traumatic canals may pass outward from a healed wound through many annual rings. In one instance horizontal canals extended through thirty-eight rings of growth, ending in another

vertical series of ducts, and from this vertical series again other horizontal ducts passed outward beyond the limits of the piece of wood at my disposal. In another case I was able to follow the course of a horizontal duct through over seventy annual rings before it finally tapered off and ended blindly. Although the horizontal canals always start from a vertical series, they by no means always end in the next outward vertical series, even when one is present. More frequently they end blindly, as in the one last described above. The formation of new series of vertical canals may recur in remote rings of growth, and these are nearly always united by horizontal canals.

It will be convenient at this stage to consider more particularly the structure of the wood parenchyma, since it is of considerable diagnostic importance. Our *fig. 2* shows the scantiness of the parenchyma as seen in transverse section through the wood, and also that it occurs on the face of the summer wood. Both these features are unusual, for in the living Sequoias the resiniferous parenchyma is particularly abundant and is found throughout the annual ring. Our fossil also presents a contrast in this respect to the woods of other extinct Sequoias. PENHALLOW[4] describes his *S. Langsdorfii* as having abundant resin cells throughout the annual ring and appearing also in a rudimentary form on the face of the summer wood. In another species, *S. Burgessii*, according to this author,[5] resin cells abundant throughout the ring are most numerous on the face of the summer wood. In the *S. magnifica* of KNOWLTON[6] the distribution of resin cells throughout the annual growth seems to be somewhat uniform. Longitudinal sections of the wood of the species under discussion, taken in numbers both in the tangential and radial planes, show clearly that the absence of resin cells from all locations except the face of the summer wood is not due to disappearance through decay, for there is no evidence of the existence of parenchymatous elements elsewhere than on the face of the summer wood. *Fig. 11* shows the appearance of the resin cells of our species in longitudinal section. They are long narrow elements comparable among living species to those of *S. gigantea*

[4] PENHALLOW, D. P., Notes on Tertiary plants. Trans. Roy. Soc. Canada **9**.

[5] *Op. cit.*

[6] KNOWLTON, F. H., Geology of the Yellowstone Park. Monographs of U. S. Geological Survey **32**: pt. 2.

rather than to the stouter, shorter similar elements of *S. semper-virens*. They may be seen on the outside of the summer wood in two contiguous annual rings. They contain a very small number of resinous globules. On the left of the figure is a longitudinal section of a vertical resin canal.

In *fig. 12* is seen a longitudinal section of a medullary ray of the species under consideration. The lateral walls of the ray which are in contact with the tracheids are characterized by so-called bordered pits, which owe their double contour to the fact that the outline of the pit on the side of the tracheid is different from that on the side of the medullary ray cell. The medullary ray of the present species of Sequoia is strikingly different from that of the two living species in features other than the crucial one of the lateral bordered pits. There are distinctly differentiated marginal cells, broader than the central cells and having two to three radial rows of pits instead of the single row found in the central cells. The marginal cells are further particularized by their undulating borders, the tops of the undulations corresponding to the walls of the tracheids. They present an additional contrast to the central cells in the fact that they are generally without tanniniferous contents and often contain very large clinorhombic crystals, lodged in cysts derived from the cell wall. The presence of crystals finds a parallel in the genus Abies among the Abietineae. STRASBURGER has noticed their occasional presence in *Abies pectinata*. I have found them to be very numerous in *A. concolor* and fewer in *A. grandis, A. bracteata, A. nobilis,* and *A. magnifica*. In Abies the crystals may or may not be associated with a dark brown matrix similar to that found in the resin cells of cupressineous woods and in the so-called crystallogenous cells which occur in the phloem of many of the Coniferales; but I have not found them inclosed in cysts derived from the cell wall as they are in the fossil species of Sequoia here described. Where the medullary rays are very deep the specialized marginal cells, instead of constituting a single row on the upper and lower borders of the ray, as is shown in our *fig. 12*, may be present to the number of three or four rows. In deep rays specialized cells may also occur in the middle of the ray, just as is occasionally the case with the tracheidal cells in the rays of certain Abietineae. Another feature which differentiates our species

from the living species of Sequoia is the very abundant pitting of the tangential walls of the medullary ray cells. This is an additional point of resemblance to the Abietineae. Through the kindness of Professor PENHALLOW I have had the opportunity of examining the type specimens of his *Sequoia Langsdorfii* and *Sequoia Burgessii*. The state of preservation of the medullary rays is very indifferent in these species; but so far as could be made out they do not possess the peculiar marginal cells and the strong pitting of the terminal (tangential) walls which are characteristic of our species. The *Sequoia magnifica* of KNOWLTON has badly preserved medullary rays, according to the author's description.[7] Professor PENHALLOW has seen sections of our species and agrees that it is new and unlike any which have been described. The name *Sequoia Penhallowii* is proposed for it in recognition of Professor PENHALLOW's great services to the paleobotany of the Coniferales. The following is the diagnosis:

### Sequoia Penhallowii, n. sp.

*Transverse.*—Rings of growth rather narrow, with sharply marked but thin summer wood. Rings regular, or if varying in thickness varying uniformly and without violent transitions except as the result of injury. Resin canals present in both the vertical and horizontal planes apparently only as the result of injury. The resin canals when present surrounded by resin cells, containing dark brown resin. Resin cells inconspicuous and confined to the face of the summer wood, except in the case of injury, where they may be present throughout the zone of annual growth. Tracheids of the spring wood very large and with pits on the radial walls only. Tracheids of the summer wood with tangential pits.

*Radial.*—Rays without tracheidal cells, but with distinctly differentiated marginal cells. Lateral pits of ray cells elliptical and bordered, larger in marginal cells. Rows of pits single in the central cells of the ray and two to three seriate in the marginal cells. Medullary ray cells covering one to four tracheids, the central ones resiniferous, the marginal generally empty, sometimes containing large clinorhombic crystals inclosed in cysts derived from the cell walls. Marginal cells with undulating free border, deeper than central cells. End walls of the cells of the medullary rays very strongly pitted. Longitudinal walls of ray cells also pitted and rather thick. Rays contain resin canals in the case of injury, which take their origin from similar vertical canals running in the wood. Resin canals of the rays sometimes ending blindly and sometimes in a more external series of vertical canals, often extending through many annual rings, varying greatly in size and frequently occluded by tyloses. Spring tracheids generally with two rows of opposite pits, which often alternate in the ends.

7 *Op. cit.*

*Tangential.*—Rays of one kind only in uninjured parts of the wood. Fusiform rays present with linear rays in the case of injury and varying greatly in size. Fusiform rays when present generally with central resin canal, which is often occluded by tyloses. Linear rays varying greatly in depth. No pits on the tangential walls of the spring tracheids. Pits on the tangential walls of the summer tracheids numerous, generally not in rows.

## CONCLUSIONS.

The greatest interest connected with the study of any extinct species is the light it throws on the structure and relationships of living forms. In the case of *Sequoia Penhallowii* the first point in this connection is its affinity with the living species of the genus. The very regular rings of growth and the very thin summer wood find their nearest parallel in *S. gigantea*. It is possible, however, that this similarity in structure of the wood may be due only to a similar mountainous habitat, since such surroundings tend, as is well known, to produce regular growth rings in living trees. For example, wood of spruce grown at high altitudes is particularly fitted for turning and the manufacture of fiddles on account of the regularity of the annual rings. The narrowness of the zone of summer wood, however, cannot be explained in this fashion. The long narrow resin cells of the wood in our species also most nearly resemble those of *S. gigantea*. The wide spring tracheids with their double rows of radial pits present a feature of resemblance to *S. sempervirens* rather than to *S. gigantea;* but this feature cannot be regarded as conclusive, since in some of the fossil Sequoias known only by impressions the larger free leaves of the *S. sempervirens* type were correlated with cones likes those of *S. gigantea.* The greater transpiration thus indicated may well have been provided for by broader and more numerously pitted tracheids. A very strong argument for the association of our species with *S. gigantea* is the fact of their similarity of geographical distribution, for the fossil under discussion came from a cañon of the Sierra Nevada Mountains, which are the home of the living *S. gigantea*. The weight of evidence seems to point to *Sequoia Penhallowii* being somewhat more closely allied to *S. gigantea* than to *S. sempervirens*.

We may now turn to the question of the light which the study of the present species throws on the general problem of the phylogeny

of the Coniferales.   Attention has been called in the descriptive part of this article to the striking points of structural resemblance presented by *S. Penhallowii* to certain abietineous species.   The medullary rays, for example, although they lack the marginal tracheidal cells characteristic of the typical Abietineae, have distinctly differentiated marginal cells which find a close parallel in the medullary rays of the genus Abies.   Further, the marginal cells of the medullary rays of our species are crystallogenous, as are those of Abies.   Another feature of strong resemblance to the Abies and the Abietineae is the marked pitting of the terminal walls of the medullary ray cells.   This character is absent or poorly marked in the cupressineous series. Equally strong indications of abietineous affinities are to be found in the structure of the wood.   The resin cells, which are such a marked feature of cupressineous woods, are almost absent in our species.   The few which are present are confined to the outer surface of the summer wood, as in the abietineous genera Tsuga and Abies.   The strongest argument, however, for the transitional nature of our fossil is that presented by the ligneous resin ducts.   As has been pointed out in the foregoing paragraphs, resin canals occur in both the horizontal and vertical planes in the wood of *S. Penhallowii* as the result of injury.   In this feature it presents a striking resemblance to the normal state of affairs in the abietineous genera Pinus, Picea, Pseudotsuga, and Larix.   In another place[8] I have pointed out that the normal occurrence of vertical resin canals in the wood of the cone, cone scales, peduncle, and *first* year's growth of strong branches of sexually mature trees of *S. gigantea* is good evidence that this species had come from ancestry characterized by the presence of ligneous resin canals.   In both *S. gigantea* and *S. sempervirens* resin canals of the vertical type only occur in the secondary wood as the result of injury.   In view of the conditions found normally in *S. gigantea* in the matter of the occurrence of resin canals, I have argued that traumatic resin canals are a case of reversion in the injured wood of *S. gigantea* and *S. sempervirens*.   Here we have an example of the value of experimental morphological evidence when confirmed by that of comparative anatomy.   Further it may be pointed out that

8 JEFFREY, E. C., The genus Sequoia. Memoirs of the Boston Society of Natural History **5**: no. 10.

if it is possible to recall experimentally morphological characters, which have entirely disappeared (as in the case of the ligneous resin ducts of *S. sempervirens*), the range of possibility in tracing phylogenetic relationships will be greatly extended. In our fossil the traumatic resin ducts occur in both the horizontal and the vertical planes, and thus present a very close approximation to the condition occurring normally in Pinus. There is, however, a difference in the arrangement of the canals, for in Pinus they are distributed regularly throughout the wood and form an anastomosing system, while in *S. Penhallowii* the vertical canals are confined to remote annual rings and the horizontal canals form a very incomplete system of connecting commissures. It is interesting to note that *S. Langsdorfii* as described by PENHALLOW has only vertical canals, while *S. Burgessii* described by the same author has only radial ones. Had the material of the latter species been as abundant and as easily manipulated as in the case of our fossil, I am disposed to think that vertical canals would have been found as well. It is a noteworthy fact that in three out of the four woods of fossil Sequoias which have been recently described, resin canals similar to those of the Abietineae have been found; or, to state it in another way, the oldest woods of Sequoia of which we have any reasonably complete knowledge more nearly approximate in structure the wood of the Abietineae than do those of their living descendants. This fact, taken in connection with the great geological age of the Abietineae, makes it very probable that the Sequoias, and as a consequence the Cupressineae in a broader sense, have come from an abietineous ancestry. This conclusion is quite in harmony with evidence derived from the study of the female cone, and other important data, as I have pointed out at length in a forthcoming memoir on the Abietineae.

## SUMMARY.

A fossil Sequoia from the Auriferous Gravels (Miocene) of the Sierra Nevada Mountains, although presenting features of wood structure which unite it with the living Sequoias, possesses other features which strongly suggest the Abietineae. The paucity of resin cells present only on the outer face of the summer wood, the highly developed medullary rays, and the traumatic resin canals

running both in the horizontal and vertical planes point strongly toward the Abietineae. The species is new and has been named *Sequoia Penhallowii*. It appears to be more closely allied to the living *S. gigantea*, and has, moreover, the same geographical occurrence. A formal diagnosis is given in the body of the article.

In conclusion I wish to express my obligations to Professor R. T. JACKSON for permission to investigate the material described in this article, and to Professor D. P. PENHALLOW for the opportunity of examining his type slides of fossil Sequoias.

HARVARD UNIVERSITY.

## EXPLANATION OF PLATES XVIII AND XIX.

### PLATE XVIII.

FIG. 1. Transverse section, including several annual rings and showing both horizontal and vertical resin canals in *Sequoia Penhallowii*. × 30.

FIG. 2. Transverse section of thin growth rings of same species. × 180.

FIG. 3. Tangential section of the same showing horizontal resin ducts. × 8.

FIG. 4. Transverse section through a healed wound in the wood of the same species; on the right is a horizontal traumatic resin duct; smaller traumatic ducts can be seen in the spring wood of the three annual rings abutting on the wound. × 4.

FIG. 5. Part of another section through the same wound, showing three horizontal ducts on the left; the smaller vertical ducts of the spring wood can be more clearly seen on account of the greater magnification. × 8.

FIG. 6. The central region of still another section through the same wound showing small vertical ducts in the spring wood. × 8.

### PLATE XIX.

FIG. 7. Another of the same more highly magnified from the margin of the wound. × 16.

FIG. 8. Transverse section through one of the large horizontal ducts seen in *fig. 3*. × 40.
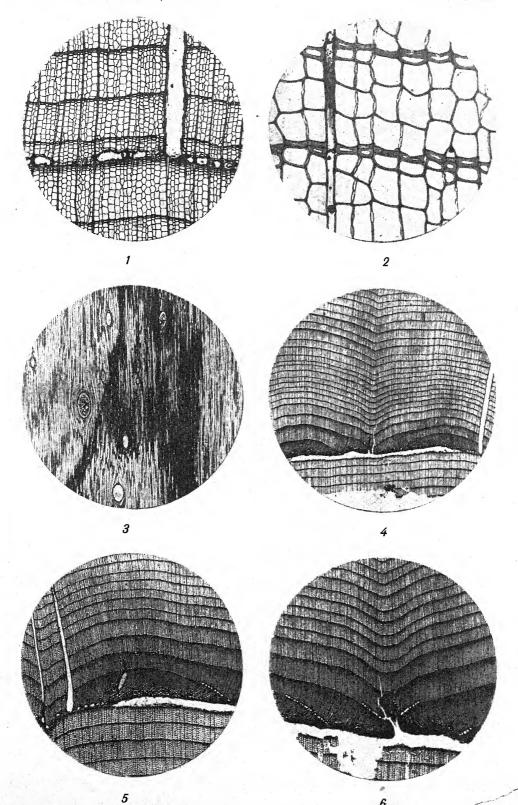
FIG. 9. Section through a smaller duct from the same preparation as that illustrated in the last figure. × 60.

FIG. 10. Section showing the relation between a horizontal and a vertical duct; the former is blocked by a tylosis. × 50.

FIG. 11. Longitudinal section, showing the scanty resiniferous parenchyma on the face of the summer wood in two annual rings; a vertical resin canal is also shown. × 60.

FIG. 12. Radial section to show the topography of a medullary ray of medium size: on the borders of the ray can be seen the empty crystallogenous cells. × 60.
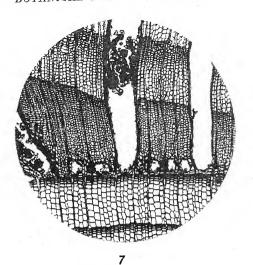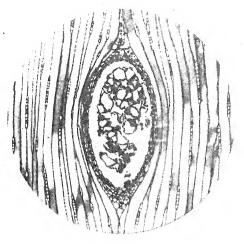
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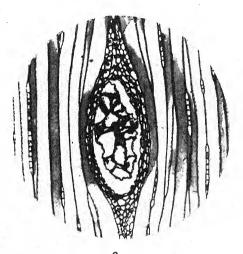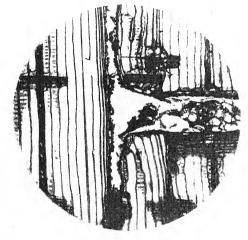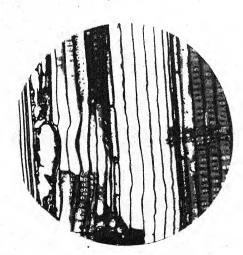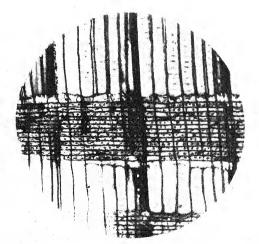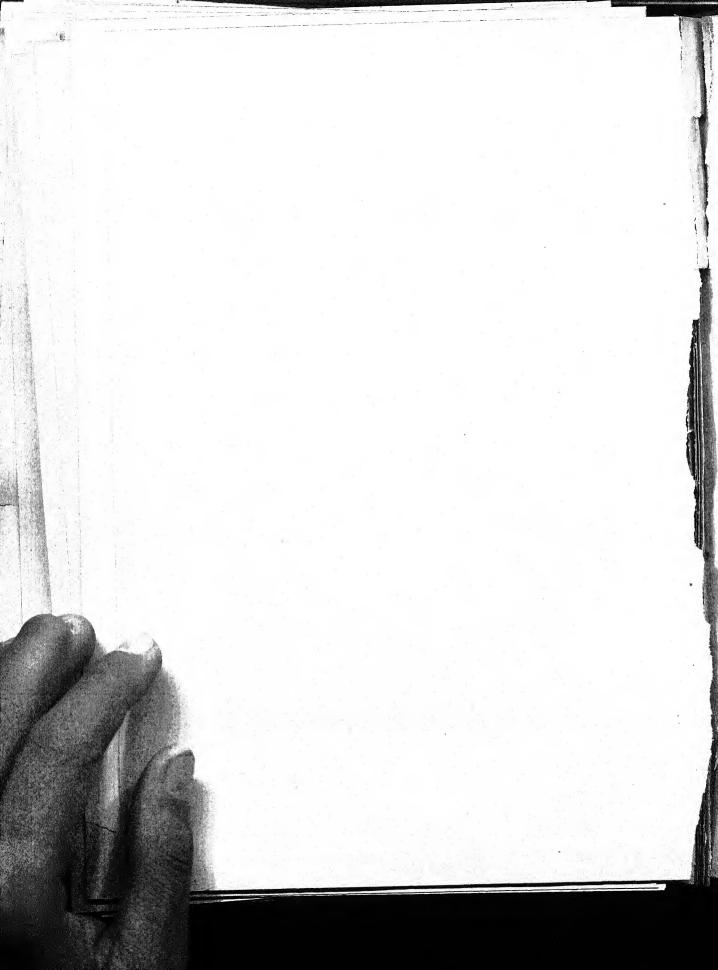
# PLACE-CONSTANTS FOR ASTER PRENANTHOIDES.

## CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXIV.

GEORGE HARRISON SHULL.

(WITH EIGHTEEN FIGURES)

### I. INTRODUCTION.

GEOGRAPHIC isolation has long been accredited as an important factor in the process of evolution, but with the introduction of methods calculated to demonstrate the evolutionary processes an altogether new conception has been gained regarding the importance of locality as a modifying factor. Statistical methods have shown that the organisms of any species from different stations, often quite near each other, are not to be considered homogeneous, and that in order to establish a proper basis for comparison investigations must deal with definite areas. The modal condition of any species prevailing on such a limited area is known as a "place-mode" for that species at that place.

The importance of determining and recording place-modes for various species was first emphasized by DAVENPORT (1899a), and in response to his appeal a considerable number of local statistical studies have been made. Some of these studies have shown that the determination of place-constants is not so simple a problem as was at first supposed. As a result of my earlier studies on Aster (SHULL 1902) it was shown that the establishment of place-constants for a species of Aster would involve the collection of all the heads produced during the season, since there is a continuous and more or less regular change in the variable characters from day to day throughout the season. It was suggested there that considerable differences might also be presented by the same population from season to season. The results of a number of studies on various species by other investigators, both before and since my study of Aster, either lead to the same conclusion or admit of the same explanation (BURKILL 1895, MACLEOD 1899, LUDWIG 1901, TOWER 1902, YULE 1902, PEARSON 1903, REINÖHL 1903, etc.).

TOWER (1902) discusses the bearing of these results upon the establishment of place-constants, and concludes "that the 'place-mode' for a species or for a character of a species should represent the average prevailing condition at a given place during a period of observation continued through years or long enough to eliminate the effect of secular fluctuations."[1]

It has been proved conclusively that conditions of variability which are a function of place are masked by others associated with time, and before we can satisfactorily arrive at the one the other must be eliminated. In the efforts which have thus far been made to establish place-constants this fact has not been taken into account. Indeed, we do not yet know how to take it into account, since no adequate investigation has been made of changes in variability which take place during the season and from season to season. It was to add to our knowledge of such secular variation and to contribute by its elimination to the establishment of true place-constants that the present study was undertaken.

[1] In his summary TOWER gives the following definition: "A 'place-mode' is the average prevailing state of a homogeneous lot of individuals [*i. e.*, of the same pleomorphic condition and stage of development] characteristic of a particular place and season, as determined by observations carried on long enough to eliminate the effects of secular climatic fluctuations." The limitation of a place-mode to a *particular season* was plainly unintentional, as it is inconsistent with the requirement that the observations be carried on long enough to eliminate the effects of secular climatic fluctuations.

PEARSON (1902) objects to this definition as not being biometric. He says: "It might refer to any constant whatever of the frequency—to the mean, the mode, the variability, or indeed to the whole frequency distribution itself." TOWER's application of the term place-*mode* to the *average prevailing condition* of a homogeneous population is in harmony with a well-known philological principle which has wrested very many words from their original signification to meanings of greater or less inclusiveness, because the original concept as limited by the literal meaning of the symbol used proved to be of comparatively little importance. In very many instances the *mode* is the least important constant involved, and in others—particularly in the variation of plants—the theoretical mode is at present indeterminable. As no one thought, in studying place-modes, of limiting his studies to the theoretical *mode*, it was not unnatural so to extend the meaning of place-mode as to involve all the quantitative relations of a population.

While it was evidently DAVENPORT's intention in proposing the word "place-mode" to use it in its strict mathematical sense, a reference to his definition will show how easy it was to make it include the entire condition of the population. He says (1899*a*): "I use the word 'place-mode' to embody a well-known idea, namely that a

## II.  MATERIAL AND METHODS.

This study is based upon the flowering heads of *Aster prenan-thoides* Muhl. collected thrice a week from the same area which furnished the serial collections for my earlier studies (SHULL 1902). This species is in some ways an ideal subject for studies of this kind. The heads are beautifully regular, as may be seen in *fig. 1*.   They are little subject to injuries, and almost the only heads which must

be thrown away are those in which insect larvae have hatched and subsisted upon the developing flowers.  Such cases are not numerous, amounting to less than 2 per cent. of the heads collected this year.

The personal equation was eliminated in the same manner as in my former work, *i. e.*, by the collection of every head that bloomed on a naturally circumscribed area.  The method used in making the counts was also the same, the heads being completely dissected.   This method prevents the errors which will frequently occur in the counting of rays without complete dissection — errors

FIG. 1.—*Aster prenanthoides* at Clifton, Ohio.

species has a different *mode* (*i. e.*, a different *prevailing* condition of size, color, etc.) in different localities.   The person who seeks to determine a place-mode determines the prevailing dimension of the principal measurable qualities (and practically all qualities of organisms are measurable) of a species as it occurs in the locality in question."

It seems desirable in applying the exact methods of the mathematician to biology to retain the exact mathematical significance of the word "place-mode," though the term then becomes of comparatively little usefulness.  As a more inclusive term, involving the characteristics of any or all the measurable qualities of a species as represented by a lot of individuals occurring at any place in question, let us adopt the word *place-condition* or *place-habit*.  We may then say that we investigate the place-habit or place-condition of a species at a particular place in order to determine or establish the place-constants, among these being the place-mode.

resulting from the loss of rays due to age or other causes—and it saves the necessity of discarding any material on this ground, since the remains of the ray-flowers are always distinguishable from the disk-flowers when they are separated.

It ought not to be necessary in work of this kind to give assurance that no material has been arbitrarily discarded, either in collection or in seriation, but the importance of this matter seems to be too little appreciated. If one student arbitrarily discards material, who else in working over the same material will arbitrarily discard on the same basis? And if an investigation cannot be repeated by another investigator with at least approximately identical results, of what value is it? TOWER (1902) assumed that his failure to get a mode at 34 in *Chrysanthemum Leucanthemum* might be due to the fact that he discarded a number of heads on account of age. He states that counts of some of this rejected material showed that all of the heads had a large number of rays. What would have been the result had he counted all the heads he rejected? Miss SMALL-WOOD (1903) "arbitrarily threw out the small" specimens of beach-flea and then presented statistics as to the size and variability of the remainder, as if these data could have either interest or scientific value.[2] If anomalies appear when all the data are seriated, they should be explained if possible, but explained or unexplained the data should be given, because these have value whether the explanation has or not.

In calculating the various constants I have again used the formulae tabulated in DAVENPORT'S (1899b) *Statistical methods*, except that instead of DUNCKER'S method of calculating the coefficient of correlation I have used the neat method adopted by YULE (1897), which may be expressed by the formula

$$\rho = \left( \frac{\Sigma f x' x''}{n} - \nu_1{}' \ \nu_1{}'' \right) \frac{1}{\sigma' \ \sigma''},$$

in which $x'$ and $x''$ are the deviations from an integral assumed mean of subject and relative classes respectively, $f$ is the frequency of occurrence of each combination of subject and relative deviations,

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[2] In justice to Miss SMALLWOOD it should be said that her paper deals chiefly with the ethological relations of the beach-flea, and that she seems to have appreciated the unsatisfactory character of her quantitative results.

$n$ is the whole number of variates, $v_1'$ and $v_1''$ are the deviations of the assumed means from the true means, and $\sigma'$ and $\sigma''$ the errors of mean square or "standard deviations" respectively of the subject and relative categories.[3]

### III.   LOCALITY AND HABITAT.

Flowers collected from the hillsides differ in a marked way from those of the same species collected in the lowlands of the same locality, as has been shown in many instances by DE VRIES, LUDWIG, REINÖHL, and others.   This is a question of habitat.   It remains an unsolved problem whether plants are not so sensitive to edaphic and local climatic conditions as to make impossible the derivation by statistical methods of anything more fundamental than the fact and the degree of this extreme sensitiveness.   This problem can be solved only by long and carefully conducted investigations.   In order that we may discriminate between the influences of habitat and locality in making studies in variation, it becomes necessary to record as carefully as possible the habitat in which the material has been collected, and so to indicate the locality that future investigators may visit the identical area studied.

The definite character both of habitat and of locality has strongly commended the choice of this particular area of *Aster prenanthoides* for such thorough investigation as is needed to elucidate the complex problems involved in work of this kind.

Clifton is a small village on the boundary between Clark and Greene counties, Ohio, in lat. 39° 48' 43'' north and long. 83° 48' 41'' west.   The Little Miami River, on whose northern bank the village lies, occupies a post-glacial channel in massive gray Niagara limestone, forming a deep and narrow gorge widely known for the beauty of its scenery.   About one kilometer west of the village two small streams enter the river from the north.   Both of these tributary streams have cut gorges in the limestone, but, being unable to corrade their beds so rapidly as does the river, they have been left high above the level of the river in hanging valleys.   At about 10–20 m from the river the Yellow Springs turnpike crosses these streams by two stone arches.   The area chosen as the source of material for this study is

[3] This method displaces DUNCKER's method in the second edition of DAVENPORT's *Statistical methods* which has just appeared.

that portion of the more westerly tributary ravine lying between the road and the precipice over which the stream falls into the river. The locality is indicated by a star on the map (*fig. 2*).

An important theoretical consideration is the relation of the locality to the whole range of the species and to the direction of its migration.
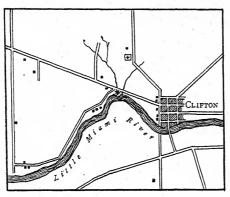


FIG. 2.—Map of Clifton and vicinity; station for *Aster prenanthoides* marked with a star.

What relation does the variability of a species near its limit of range bear to that at its center? Is there a progressive change of variable characters along the lines of migration radiating from the center of distribution of the species? ADAMS (1902) accepts such progressive change as one of his ten criteria for the determination of centers of distribution. He concludes that the southeastern United States has been the principal center of post-glacial distribution for the eastern half of North America. The determination of place-constants in various parts of the range would test the value of this criterion. It is to be hoped that investigators in other places will make studies similar to this for the purpose of throwing a more certain light on these principles.

To show the relation of Clifton, Ohio, to the total range of *Aster prenanthoides* I present in *fig. 3* a map showing the range of the species as represented at the present time by specimens in the leading American herbaria. Such a map is always to some extent a commentary on the limitations of the herbaria, and does not correctly represent the relative frequency of the species in the different parts of its range. E. S. BURGESS, the well-known specialist on the genus Aster, writes that the stations in the Berkeley Hills, Mass., and in the Catskills and Shawangunk Mountains, N. Y., are really extralimital, "the species becoming common 300 miles [480 km] westward, and reaching proper development along the southern shore of Lake Erie and thence through western Pennsylvania." The fewness of

the stations in the western half of the range is due to the general scarcity of herbarium material from this area rather than to the rarity of the species. It will be seen from this map that the Clifton station (marked with a star) is very nearly central.



FIG. 3.—The range of *Aster prenanthoides* as represented by specimens in the leading American herbaria;[4] Clifton, Ohio, marked with a star.

[4] The stations represented on the map are as follows: MASSACHUSETTS: Berkeley Hills. NEW YORK: Chenango Co., Oswego Co., Tompkins Co., Andover, Big Tree, Bridgewater, Buffalo, Elmira, Macedon, Catskill Mts., Shawangunk Mts. NEW JERSEY: Woodbury. PENNSYLVANIA: Bedford Co., Chester Co., Conewago Co., Lancaster Co., Westmoreland Co., Easton, Mercersburg, Philadelphia, Trout Run. MARYLAND: Baltimore, Emmittsburg. DISTRICT OF COLUMBIA: Washington. VIR-GINIA: Big Stone Gap, Pulaski, Wytheville. WEST VIRGINIA: Aurora. KENTUCKY:

The habitat of the population in question is typical of the species, if we may judge from the statements made in the various manuals, all of which agree that the characteristic habitat is along margins of streams in shady places. This fact will make it easy to find these plants growing under essentially the same conditions in other localities, and thus facilitate the establishment of place-constants which shall be



FIG. 4.—The habitat, looking south.

properly comparable. The general character of the habitat at Clifton will be best understood by a reference to *figs. 1, 4,* and *5.* It will be at once recognized that we have here an example of temporary mesophytic climax characteristic of young ravines, the luxuriance of vegeta-

Bell Co., Carter Co., Lexington. Oнιo: Franklin Co., Berea, Cleveland, Clifton, Ironton, Mansfield, Wooster. INDIANA: Hamilton Co. ILLINOIS: Canton. MICHIGAN: Allegan Co., Keweenaw Co. WISCONSIN: Eau Galle, Milwaukee, Racine, Sparta. MINNESOTA: Mazeppa. IOWA: Fayette Co., Johnson Co., Ames. KANSAS: Neosho Co.

tion being due to the moderation of extremes of temperature, light, etc., the protection from winds, and the consequent maintenance of a relatively high degree of humidity.   Besides the relative constancy of atmospheric conditions, it should be noted that the stream which occupies the ravine, and along whose margin the *Aster prenanthoides* is growing, is a permanent, spring-fed stream draining so small an
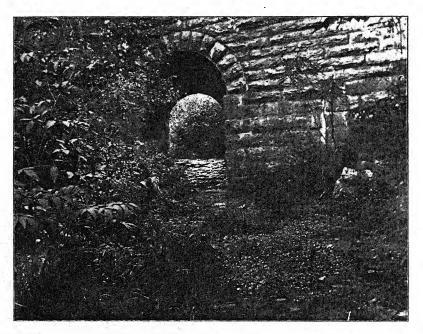


FIG. 5.—The habitat, looking north.

area as to be little subject to fluctuations due to the alternations of dry and rainy periods.   The map shown in *fig. 6* accurately represents the present position of the stream and the location of the areas of *Aster prenanthoides* with reference to it, thus enabling the future investigator to note any changes of area or relation which might have an influence upon the variability.

## IV.   RESULTS.

The collections having been made about three times a week, regardless of the number of heads which were in bloom at any time, it does not seem desirable to present curves and correlation tables
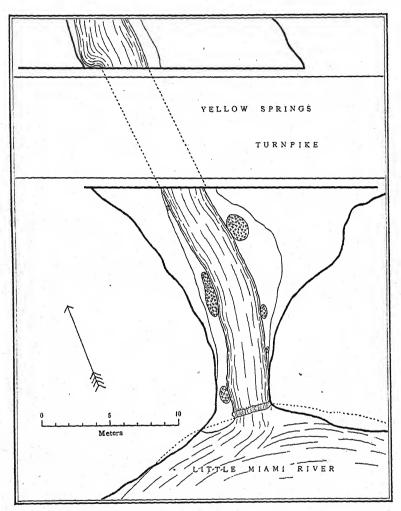
FIG. 6.—Map showing the relation of *Aster prenanthoides* to the stream at the Clifton station; heavy contours represent the upper margin of the cliffs; light contours show the limit of the flood plains; depth of ravine 5–7 m; height of hanging valley above river level 7–8 m.

of each separate collection. In order to make the original data available for any purpose to which other students may wish to turn it, I give in tabulated form the results of the several collections (Tables A, B, and C).

## TABLE A.

BRACTS.

| No. | SEPTEMBER, 1903 | | | | | | | | | OCTOBER, 1903 | | | TOTAL 1903 | 1900 IN % | 1903 IN % | SUM IN % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 12 | 14 | 16 | 18 | 21 | 23 | 25 | 28 | 30 | 2 | 6 | 9 | | | | |
| 18 | .. | .. | .. | .. | .. | .. | I | .. | .. | .. | .. | .. | I | .... | .13 | .07 |
| 19 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .... | .00 | .00 |
| 20 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | I | .. | I | .... | .13 | .07 |
| 21 | .. | .. | .. | .. | .. | .. | .. | .. | I | .. | .. | .. | I | .... | .13 | .07 |
| 22 | .. | .. | .. | .. | I | .. | I | .. | .. | I | .. | .. | 3 | .... | .40 | .21 |
| 23 | .. | .. | .. | I | .. | .. | I | 2 | .. | .. | .. | .. | 4 | .... | .53 | .28 |
| 24 | I | .. | .. | .. | I | .. | I | 2 | .. | .. | .. | I | 5 | .... | .66 | .35 |
| 25 | I | .. | I | .. | I | I | .. | .. | .. | .. | I | .. | 6 | .... | .79 | .42 |
| 26 | 2 | .. | .. | I | I | I | .. | I | 2 | .. | I | .. | 9 | .... | 1.19 | .64 |
| 27 | .. | .. | .. | .. | .. | 2 | .. | 2 | .. | I | 5 | .. | 10 | .... | 1.32 | .71 |
| 28 | 2 | I | .. | .. | 3 | I | .. | .. | I | 6 | 7 | .. | 21 | .... | 2.77 | 1.48 |
| 29 | 5 | .. | .. | I | I | I | I | 3 | 4 | 5 | 9 | .. | 30 | .30 | 3.96 | 2.26 |
| 30 | 4 | 2 | .. | I | .. | .. | 2 | 6 | 4 | 5 | 6 | .. | 30 | .46 | 3.96 | 2.33 |
| 31 | 3 | 2 | .. | I | .. | I | .. | 5 | 3 | 9 | 4 | .. | 28 | .15 | 3.70 | 2.05 |
| 32 | 2 | I | .. | 2 | 3 | 4 | .. | 9 | 2 | 6 | 7 | .. | 36 | 1.22 | 4.75 | 3.11 |
| 33 | I | .. | .. | .. | .. | 3 | 2 | 10 | 4 | 5 | 10 | 2 | 37 | .76 | 4.88 | 2.97 |
| 34 | 2 | I | .. | I | 5 | 4 | 6 | 8 | 2 | 7 | 6 | .. | 42 | 2.43 | 5.54 | 4.10 |
| 35 | .. | 2 | I | 3 | 2 | 6 | .. | 4 | 7 | 4 | 4 | .. | 33 | .91 | 4.36 | 2.76 |
| 36 | .. | .. | .. | 5 | 2 | 5 | 3 | 6 | 6 | 5 | I | .. | 33 | 2.28 | 4.36 | 3.39 |
| 37 | .. | .. | I | I | I | I | 4 | 10 | 4 | I | 6 | .. | 29 | 3.50 | 3.83 | 3.68 |
| 38 | .. | I | 2 | 3 | 4 | 5 | 2 | 5 | 5 | 4 | 3 | I | 35 | 3.65 | 4.62 | 4.17 |
| 39 | I | I | 3 | 6 | .. | 4 | 3 | 7 | 4 | 4 | 4 | I | 38 | 5.62 | 5.02 | 5.30 |
| 40 | .. | .. | I | I | 2 | 3 | 2 | 3 | 3 | 5 | 2 | .. | 22 | 5.47 | 2.90 | 4.10 |
| 41 | .. | 2 | 2 | 3 | 4 | 6 | 5 | 5 | 3 | I | .. | .. | 31 | 7.30 | 4.09 | 5.59 |
| 42 | I | 2 | I | 4 | I | 3 | 3 | 5 | .. | 6 | I | .. | 28 | 5.17 | 3.70 | 4.38 |
| 43 | .. | I | .. | 2 | 4 | 9 | 4 | 6 | .. | I | .. | .. | 27 | 7.14 | 3.56 | 5.30 |
| 44 | .. | 2 | I | 2 | I | 8 | 3 | I | I | 3 | .. | .. | 22 | 6.99 | 2.90 | 4.81 |
| 45 | .. | 2 | I | 3 | I | 3 | 7 | 5 | .. | .. | I | .. | 23 | 6.54 | 3.04 | 4.67 |
| 46 | .. | .. | I | 6 | 2 | 5 | 3 | 7 | I | .. | 2 | .. | 27 | 5.02 | 3.56 | 4.24 |
| 47 | I | 3 | .. | 9 | 2 | 3 | 2 | 3 | .. | .. | I | .. | 24 | 5.32 | 3.17 | 4.17 |
| 48 | 2 | 2 | .. | 6 | 2 | 2 | 2 | 3 | .. | I | I | .. | 21 | 5.62 | 2.77 | 4.10 |
| 49 | I | 4 | 4 | 6 | 5 | 2 | 5 | .. | I | 2 | .. | .. | 30 | 6.99 | 3.96 | 5.37 |
| 50 | 3 | 4 | I | 2 | 5 | I | .. | .. | .. | I | .. | .. | 17 | 6.23 | 2.24 | 4.10 |
| 51 | .. | .. | 2 | 8 | 3 | I | I | 3 | I | .. | .. | .. | 19 | 3.04 | 2.51 | 2.76 |
| 52 | 2 | I | .. | 4 | I | 3 | .. | .. | 3 | .. | .. | .. | 14 | 2.74 | 1.85 | 2.26 |
| 53 | I | I | .. | 5 | 2 | 2 | .. | 2 | .. | .. | .. | .. | 13 | 1.98 | 1.72 | 1.84 |
| 54 | .. | I | .. | I | .. | I | .. | .. | .. | .. | .. | .. | 3 | 1.37 | .40 | .85 |
| 55 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .30 | .00 | .14 |
| 56 | I | .. | I | .. | .. | .. | .. | .. | .. | .. | .. | .. | 2 | .15 | .26 | .21 |
| 57 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .00 | .00 | .00 |
| 58 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .15 | .00 | .07 |
| 59 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .46 | .00 | .21 |
| 60 | .. | I | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | I | .30 | .13 | .21 |
| 61 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .00 | .00 | .00 |
| 62 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .00 | .00 | .00 |
| 63 | .. | .. | .. | .. | .. | I | .. | .. | .. | .. | .. | .. | I | .15 | .13 | .14 |
| 64 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .15 | .... | .07 |
| | 36 | 37 | 23 | 88 | 60 | 92 | 64 | 123 | 64 | 83 | 83 | 4 | 757 | | | |

## TABLE B.
### RAYS.

| No. | SEPTEMBER, 1903 | | | | | | | | | OCTOBER, 1903 | | | TOTAL 1903 | 1900 IN % | 1903 IN % | SUM IN % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 12 | 14 | 16 | 18 | 21 | 23 | 25 | 28 | 30 | 2 | 6 | 9 | | | | |
| 12 | .. | .. | .. | .. | .. | .. | .. | I | .. | I | .. | .. | 2 | .... | .26 | .14 |
| 13 | .. | .. | .. | I | .. | .. | .. | .. | .. | .. | .. | .. | I | .... | .13 | .07 |
| 14 | .. | .. | .. | .. | .. | .. | I | .. | I | .. | 2 | .. | 4 | .... | .53 | .28 |
| 15 | .. | .. | .. | I | I | .. | .. | .. | .. | .. | I | .. | 3 | .... | .40 | .21 |
| 16 | 4 | .. | I | I | .. | 2 | 3 | 2 | I | I | I | .. | 16 | .... | 2.11 | 1.13 |
| 17 | 2 | I | .. | .. | .. | .. | .. | 2 | .. | .. | 3 | .. | 8 | .15 | 1.06 | .64 |
| 18 | 5 | .. | .. | I | 3 | I | .. | 3 | 3 | 2 | 3 | .. | 21 | .00 | 2.77 | 1.48 |
| 19 | I | 2 | .. | .. | 4 | 3 | .. | 5 | .. | 4 | 10 | .. | 29 | .91 | 3.83 | 2.47 |
| 20 | 7 | I | .. | I | I | 3 | I | 12 | 4 | 4 | 7 | .. | 41 | .91 | 5.41 | 3.32 |
| 21 | 2 | 2 | .. | 3 | 5 | 7 | 3 | 9 | 6 | 7 | 9 | .. | 53 | 2.13 | 7.00 | 4.74 |
| 22 | I | 2 | I | 4 | 3 | 11 | 5 | 13 | 8 | 15 | 11 | .. | 74 | 5.12 | 9.77 | 7.56 |
| 23 | I | I | 5 | 5 | 3 | 8 | 5 | 12 | 6 | 7 | 6 | 2 | 61 | 5.32 | 8.05 | 6.79 |
| 24 | .. | I | 2 | 7 | 4 | 4 | 3 | 4 | 7 | 8 | 6 | .. | 46 | 7.30 | 6.07 | 6.65 |
| 25 | I | 2 | 2 | 2 | 2 | 5 | 5 | 10 | 6 | 9 | 8 | I | 53 | 7.45 | 7.00 | 7.21 |
| 26 | I | 2 | 2 | 3 | 5 | 2 | 8 | 14 | 9 | 5 | 6 | .. | 57 | 8.66 | 7.52 | 8.06 |
| 27 | .. | I | 2 | 4 | 4 | 7 | 5 | 11 | 5 | 5 | 4 | I | 47 | 8.97 | 6.20 | 7.49 |
| 28 | I | 8 | I | 2 | .. | 6 | 6 | 6 | 4 | 5 | 2 | .. | 41 | 8.36 | 5.41 | 6.79 |
| 29 | I | I | .. | 6 | 5 | 11 | 3 | 6 | I | 2 | I | .. | 37 | 7.14 | 4.88 | 5.94 |
| 30 | .. | 4 | .. | 4 | 3 | 6 | 4 | 4 | I | 4 | 2 | .. | 32 | 7.14 | 4.22 | 5.59 |
| 31 | I | 2 | 3 | 8 | I | 3 | 5 | 4 | I | 4 | .. | .. | 32 | 7.90 | 4.22 | 5.94 |
| 32 | 5 | .. | I | 8 | 2 | 2 | 2 | 3 | 2 | .. | .. | .. | 25 | 6.23 | 3.30 | 4.67 |
| 33 | .. | 2 | .. | 12 | 6 | 7 | 3 | I | .. | .. | .. | .. | 31 | 7.45 | 4.09 | 5.66 |
| 34 | .. | I | I | 8 | 2 | 3 | .. | I | .. | .. | .. | .. | 16 | 5.02 | 2.11 | 3.46 |
| 35 | 2 | I | I | 4 | 5 | .. | I | .. | .. | .. | I | .. | 15 | 1.67 | 1.98 | 1.84 |
| 36 | I | 2 | I | 2 | I | I | .. | .. | .. | .. | .. | .. | 8 | 1.22 | 1.06 | 1.13 |
| 37 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .15 | .00 | .07 |
| 38 | .. | .. | .. | I | .. | .. | I | .. | .. | .. | .. | .. | 2 | .46 | .26 | .35 |
| 39 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .15 | .00 | .07 |
| 40 | .. | I | .. | .. | .. | .. | .. | .. | I | .. | .. | .. | 2 | .15 | .26 | .21 |
| 41 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .00 | .... | .00 |
| 42 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | ., | .. | .15 | .... | .07 |
| | 36 | 37 | 23 | 88 | 60 | 92 | 64 | 123 | 64 | 83 | 83 | 4 | 757 | | | |

## TABLE C.
### DISK-FLORETS.

| No. | SEPTEMBER, 1903 | | | | | | | | | OCTOBER, 1903 | | | TOTAL 1903 | 1900 IN % | 1903 IN % | SUM IN % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 12 | 14 | 16 | 18 | 21 | 23 | 25 | 28 | 30 | 2 | 6 | 9 | | | | |
| 14 | .. | .. | .. | .. | .. | .. | .. | .. | I | .. | .. | .. | I | .... | .13 | .07 |
| 15 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .... | .00 | .00 |
| 16 | .. | .. | .. | .. | .. | .. | I | .. | .. | .. | .. | .. | I | .... | .13 | .07 |
| 17 | .. | .. | .. | I | .. | .. | .. | .. | .. | .. | .. | .. | I | .... | .13 | .07 |
| 18 | .. | .. | I | .. | .. | .. | .. | I | .. | .. | .. | .. | 2 | .... | .26 | .14 |
| 19 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .... | .00 | .00 |
| 20 | I | .. | .. | .. | .. | .. | .. | .. | .. | I | .. | .. | 2 | .... | .26 | .14 |
| 21 | .. | .. | ., | .. | .. | .. | .. | .. | .. | .. | I | .. | I | .... | .13 | .07 |
| 22 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .... | .00 | .00 |
| 23 | .. | .. | .. | .. | .. | .. | I | .. | .. | .. | I | .. | 2 | .... | .26 | .14 |
| 24 | .. | .. | .. | .. | .. | .. | .. | .. | I | .. | .. | .. | I | .... | .13 | .07 |
| 25 | .. | .. | .. | .. | .. | .. | .. | I | .. | .. | I | .. | 2 | .15 | .26 | .21 |

TABLE C (*continued*).

| No. | September, 1903 | | | | | | | | | October, 1903 | | | Total 1903 | 1900 in % | 1903 in % | Sum in % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 12 | 14 | 16 | 18 | 21 | 23 | 25 | 28 | 30 | 2 | 6 | 9 | | | | |
| 21 | .. | .. | .. | .. | .. | .. | I | .. | 2 | .. | I | .. | 4 | .00 | .53 | .28 |
| 27 | .. | .. | .. | .. | .. | I | .. | 2 | .. | I | .. | .. | 4 | .00 | .53 | .28 |
| 28 | I | .. | .. | .. | 2 | .. | .. | I | .. | I | 3 | .. | 7 | .00 | .92 | .49 |
| 29 | I | .. | .. | .. | .. | 2 | .. | .. | I | I | 4 | .. | 9 | .00 | 1.19 | .64 |
| 30 | 3 | .. | .. | .. | I | .. | .. | .. | .. | I | 5 | .. | 10 | .00 | 1.32 | .71 |
| 31 | 2 | .. | .. | .. | 2 | I | I | 3 | .. | I | I | .. | 11 | .15 | 1.45 | .85 |
| 32 | .. | .. | .. | .. | 2 | 3 | I | 3 | .. | :: | I | .. | 10 | .15 | 1.32 | .78 |
| 33 | I | I | .. | .. | I | .. | .. | 2 | .. | 5 | 2 | .. | 12 | .15 | 1.58 | .92 |
| 34 | I | .. | .. | 4 | .. | 2 | .. | I | 3 | I | 3 | .. | 15 | .46 | 1.98 | 1.27 |
| 35 | 3 | I | .. | I | I | 2 | I | 5 | 2 | 4 | 9 | I | 30 | .15 | 3.96 | 2.19 |
| 36 | .. | I | .. | 2 | I | 2 | I | 4 | I | 4 | 5 | .. | 21 | .00 | 2.77 | 1.48 |
| 37 | 2 | .. | 2 | I | 5 | 2 | I | 4 | 3 | 3 | 6 | .. | 29 | .46 | 3.83 | 2.26 |
| 38 | 3 | .. | .. | 2 | I | I | 3 | 4 | 3 | 6 | 4 | .. | 27 | .46 | 3.56 | 2.12 |
| 39 | 2 | 3 | 3 | I | I | 3 | 3 | 5 | 3 | 5 | I | .. | 30 | .61 | 3.96 | 2.40 |
| 40 | 2 | I | .. | 2 | 2 | 2 | I | 5 | .. | 4 | 4 | .. | 23 | 1.98 | 3.04 | 2.55 |
| 41 | I | .. | .. | 2 | I | 2 | 2 | 8 | 3 | 4 | 5 | 2 | 30 | 1.22 | 3.96 | 2.69 |
| 42 | .. | 2 | I | 4 | .. | 5 | .. | 9 | 4 | 6 | 3 | .. | 36 | 2.28 | 4.75 | 3.61 |
| 43 | 2 | I | .. | 2 | I | 4 | .. | 6 | 2 | 2 | 2 | .. | 22 | 4.10 | 2.90 | 3.46 |
| 44 | .. | .. | .. | .. | I | 5 | I | 6 | 6 | 2 | 4 | I | 26 | 3.50 | 3.43 | 3.46 |
| 45 | .. | I | 4 | 3 | 2 | 4 | 3 | 3 | 7 | 4 | 4 | .. | 35 | 5.78 | 4.62 | 5.16 |
| 46 | .. | 2 | I | I | 2 | 2 | 2 | 5 | I | 9 | I | .. | 26 | 6.54 | 3.43 | 4.88 |
| 47 | 2 | 3 | 2 | 2 | 3 | 3 | 2 | 4 | 2 | 7 | 2 | .. | 32 | 5.32 | 4.22 | 4.74 |
| 48 | .. | .. | .. | 3 | .. | 7 | 2 | 4 | 6 | 2 | I | .. | 25 | 5.93 | 3.30 | 4.52 |
| 49 | .. | 3 | .. | 3 | 3 | I | 2 | 5 | 4 | 2 | 2 | .. | 25 | 7.14 | 3.30 | 5.09 |
| 50 | .. | I | 2 | I | 2 | 2 | 3 | 9 | 4 | 3 | 4 | .. | 31 | 7.14 | 4.09 | 5.51 |
| 51 | .. | I | I | 5 | 2 | 4 | 2 | 3 | I | .. | I | .. | 20 | 5.47 | 2.64 | 3.96 |
| 52 | I | I | .. | 4 | .. | 4 | I | 5 | 2 | .. | I | .. | 19 | 6.84 | 2.51 | 4.52 |
| 53 | .. | I | I | 3 | 2 | 4 | 2 | 4 | 5 | 3 | .. | .. | 21 | 6.38 | 2.77 | 4.45 |
| 54 | .. | .. | .. | 2 | I | 4 | 5 | 2 | I | .. | I | .. | 16 | 4.86 | 2.11 | 3.39 |
| 55 | I | 3 | .. | 2 | 4 | 3 | 5 | 5 | .. | .. | .. | .. | 23 | 3.95 | 3.04 | 3.46 |
| 56 | I | 3 | I | 4 | 6 | 3 | 3 | 2 | .. | .. | .. | .. | 23 | 4.56 | 3.04 | 3.75 |
| 57 | .. | .. | .. | 3 | 3 | 8 | 2 | I | I | .. | .. | .. | 18 | 2.74 | 2.38 | 2.55 |
| 58 | .. | I | 2 | 6 | 2 | I | 4 | I | I | .. | .. | .. | 18 | 2.13 | 2.38 | 2.26 |
| 59 | 2 | .. | I | 5 | I | 4 | 2 | .. | .. | .. | .. | .. | 15 | 1.67 | 1.98 | 1.84 |
| 60 | I | I | .. | 4 | 3 | I | .. | .. | .. | .. | .. | .. | 10 | 2.13 | 1.32 | 1.70 |
| 61 | I | .. | .. | 2 | .. | I | .. | .. | .. | .. | .. | .. | 4 | 1.37 | .53 | .92 |
| 62 | .. | .. | .. | 3 | I | .. | I | .. | .. | .. | .. | .. | 5 | 1.22 | .66 | .92 |
| 63 | .. | .. | .. | .. | .. | I | .. | .. | .. | .. | .. | .. | I | .61 | .13 | .35 |
| 64 | 2 | .. | I | 2 | I | .. | I | .. | .. | .. | .. | .. | 7 | .00 | .92 | .49 |
| 65 | .. | .. | .. | I | .. | .. | .. | .. | .. | .. | .. | .. | I | 1.06 | .13 | .57 |
| 66 | .. | .. | .. | 2 | .. | .. | .. | .. | .. | .. | .. | .. | 2 | .46 | .26 | .35 |
| 67 | .. | I | .. | 2 | .. | .. | .. | .. | .. | .. | .. | .. | 3 | .00 | .40 | .21 |
| 68 | .. | .. | .. | 3 | .. | .. | .. | .. | .. | .. | .. | .. | 3 | .30 | .40 | .35 |
| 69 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .15 | .00 | .07 |
| 70 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .00 | .00 | .00 |
| 71 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .00 | .00 | .00 |
| 72 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .00 | .00 | .00 |
| 73 | .. | I | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | I | .15 | .13 | .14 |
| 74 | .. | 2 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 2 | .15 | .26 | .21 |
| 75 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .00 | .00 | .00 |
| 76 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .00 | .00 | .00 |
| 77 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 0 | .00 | .00 | .00 |
| 78 | .. | 2 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 2 | .00 | .26 | .14 |
| 79 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .15 | .... | .07 |
| | 36 | 37 | 23 | 88 | 60 | 92 | 64 | 123 | 64 | 83 | 83 | 4 | 757 | | | |

## TABLE D.

### CHIEF CONSTANTS OF THE SEVERAL COLLECTIONS.

| Bracts | Sep. 12 | Sep. 14 | Sep. 16 | Sep. 18 | Sep. 21 | Sep. 23 | Sep. 25 | Sep. 28 | Sep. 30 | Oct. 2 | Oct. 6 | Oct. 9 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean | 36.555 | 43.297 | 43.174 | 43.898 | 40.700 | 40.652 | 39.828 | 37.423 | 36.016 | 35.120 | 33.096 | 35.750 |
| P. E. M | ±1.110 | ±.868 | ±.947 | ±.500 | ±.723 | ±.492 | ±.598 | ±.401 | ±.543 | ±.423 | ±.389 | ±.935 |
| σ | 9.870 | 7.829 | 6.735 | 6.951 | 8.303 | 7.002 | 7.090 | 6.508 | 6.438 | 5.717 | 5.247 | 2.773 |
| P.E.σ | ±.785 | ±.614 | ±.670 | ±.353 | ±.511 | ±.348 | ±.423 | ±.284 | ±.384 | ±.299 | ±.275 | ±.661 |
| C.V. | 27.000 | 18.081 | 15.600 | 15.835 | 20.401 | 17.225 | 17.801 | 17.630 | 17.877 | 16.278 | 15.854 | 7.756 |
| P. E. v | ±2.146 | ±1.418 | ±1.551 | ±.805 | ±1.256 | ±.857 | ±1.061 | ±.758 | ±1.066 | ±.852 | ±.830 | ±1.849 |

| Rays | Sep. 12 | Sep. 14 | Sep. 16 | Sep. 18 | Sep. 21 | Sep. 23 | Sep. 25 | Sep. 28 | Sep. 30 | Oct. 2 | Oct. 6 | Oct. 9 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean | 23.305 | 27.540 | 26.739 | 28.681 | 26.600 | 26.033 | 26.187 | 24.179 | 24.109 | 23.880 | 22.301 | 24.500 |
| P. E. M | ±.720 | ±.582 | ±.669 | ±.380 | ±.485 | ±.326 | ±.392 | ±.249 | ±.342 | ±.272 | ±.278 | ±.559 |
| σ | 6.407 | 5.248 | 4.757 | 5.284 | 5.571 | 4.628 | 4.650 | 4.092 | 4.058 | 3.668 | 3.757 | 1.658 |
| P.E.σ | ±.509 | ±.412 | ±.473 | ±.269 | ±.343 | ±.230 | ±.277 | ±.176 | ±.242 | ±.192 | ±.197 | ±.396 |
| C.V. | 27.400 | 19.158 | 17.790 | 18.423 | 20.945 | 17.780 | 17.756 | 16.926 | 16.834 | 15.361 | 16.846 | 6.769 |
| P. E. v | ±2.185 | ±1.494 | ±1.769 | ±.937 | ±1.290 | ±.884 | ±1.059 | ±.728 | ±1.004 | ±.804 | ±.882 | ±1.614 |

| Disk-florets | Sep. 12 | Sep. 14 | Sep. 16 | Sep. 18 | Sep. 21 | Sep. 23 | Sep. 25 | Sep. 28 | Sep. 30 | Oct. 2 | Oct. 6 | Oct. 9 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean | 41.611 | 51.729 | 46.522 | 51.511 | 47.100 | 46.891 | 47.672 | 43.569 | 42.187 | 41.301 | 38.072 | 40.250 |
| P. E. M | ±1.282 | ±1.318 | ±1.343 | ±.724 | ±.862 | ±.603 | ±.813 | ±.459 | ±.682 | ±.469 | ±.535 | ±1.103 |
| σ | 11.405 | 11.884 | 9.546 | 10.062 | 9.899 | 8.569 | 9.647 | 7.539 | 8.087 | 6.339 | 7.210 | 3.269 |
| P.E.σ | ±.907 | ±.932 | ±.949 | ±.512 | ±.610 | ±.426 | ±.575 | ±.324 | ±.482 | ±.332 | ±.378 | ±.780 |
| C.V. | 27.408 | 22.973 | 20.519 | 19.534 | 21.017 | 18.274 | 20.236 | 17.303 | 19.170 | 15.349 | 18.962 | 8.122 |
| P. E. v | ±2.179 | ±1.801 | ±2.041 | ±.993 | ±1.294 | ±.909 | ±1.206 | ±.744 | ±1.143 | ±.804 | ±.993 | ±1.937 |

In Table D are given the more important constants of the several collections with the probable errors of the determination. The average deviation is omitted as having no significance, since the probable error of the determination is almost as large as the determined value of the constant. It will be noted on examining this table that all the constants are quite variable, and that only the mean seems to follow a rather definite law, beginning low, then leaping almost immediately to the maximum, after which there is a gradual fall until almost the end, when a slight rise appears. The fall of mean values from the maximum on September 18 to the minimum on October 6 was 24.6 per cent. in bracts, 22.25 per cent. in rays, and 26.4 per cent. in disk-florets. The changes of mean value for each set of variants from the beginning to the end of the flowering season and the corresponding changes observed in 1900 are shown graphically in *fig. 7*.

1. *Bracts.*—The frequency polygon for the bracts is shown in *fig. 8.* The mean value is 38.597 ± .189, and a number of empirical modes are present. Some, if not all, of these are doubtless due to the smallness of the number of heads counted. It will be noted
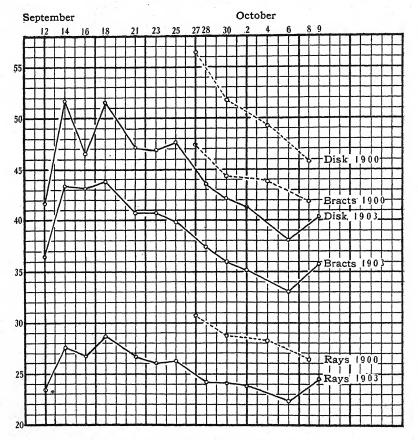


Fig. 7.—Curves showing the changes in the mean numbers of parts in the heads from the beginning to the end of the season, and the difference between the two collections, 1900 and 1903.

that the most prominent modes are those which lie below the mean value; *i. e.,* if one may speak of skewness in multimodal curves, there is evident here a strong positive skewness. The breadth of the curve exhibits to the eye the great variability, which may be expressed

numerically by the standard deviation $7.692 \pm .133$, or by the coefficient of variability $19.928 \pm .345$.

2. *Rays.*—The ray-curve shown in *fig. 9* has the mean at $25.247 \pm .122$ and by much the strongest mode at 22, so that here again there is a very prominent skewing of the curve. The empirical
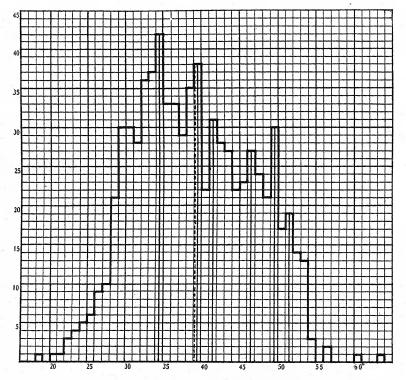


FIG. 8.—Bract-curve for 757 heads collected in 1903: mean $38.597 \pm .189$; empirical modes 29–30, 34, 39, 41, 46, 49, 51; $\sigma = 7.692 \pm .133$.

modes at 16, 22, 26, 33 are somewhat suggestive of the series which LUDWIG, DE VRIES, and others have shown to be so common, but aside from such suggestion can have little meaning. The standard deviation $4.990 \pm .087$ is considerably less than that of the bracts, while the coefficient of variability, $19.764 \pm .344$, is practically the same.
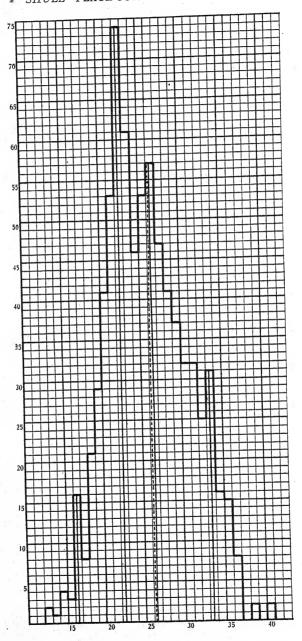
FIG. 9.—Ray-curve for 757 heads collected in 1903: mean $25.247 \pm .122$; empirical modes 16, 22, 26, 33; $\sigma = 4.9899 \pm .0865$.

3. *Disk-florets.*—The polygon of distribution of the disk-florets is presented in *fig. 10.* The range, from 14 to 78, is so wide that 757 heads are quite insufficient to make the many empirical modes of any
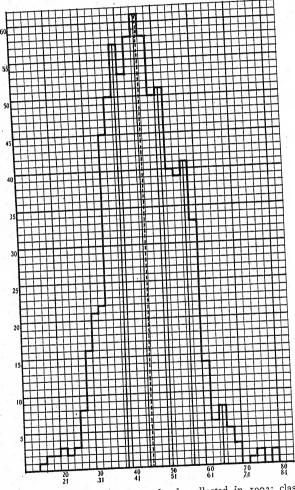


FIG. 10.—Disk-floret curve for 757 heads collected in 1903: classes doubled; mean 44.933 ± .238; empirical modes 38–39, 44–45, 50–51, 56–57, 64–65; $\sigma = 9.703$ ± .168.

significance. To make the curve comparable with that offered by the disk-florets in 1900, the classes were doubled, but this still leaves

five prominent modes. The positive skewness is not so marked as in the bracts and rays, but inspection of the curve will show plainly that the theoretical mode is below the mean, though the principal apparent mode nearly coincides with the mean. The standard deviation is 9.703 ± .168 and the coefficient of variability 21.595 ± .374.

4. *Summation, 1900 and 1903.*—The more important constants for bracts, rays, and disk-florets are given in Tables E, F, and G, along with the corresponding data for 1900 and the summation of the two lots. The summation-curves of bracts, rays, and disk-

### TABLE E.

CONSTANTS OF BRACTS FOR 1900, 1903, AND THEIR SUM.

|  | 1900 | 1903 | Combined |
|---|---|---|---|
| Number............. | 658 | 757 | 1415 |
| Mean............... | 44.044 | 38.597 | 41.130 |
| P. E. $_M$........... | ± .150 | ± .189 | ± .131 |
| Modes, empirical.... | 34, 39, 43, 49 | 29–30, 34, 39, 41, 46, 49, 51 | 30, 32, 34, 39, 41, 43, 49 |
| $\sigma$................. | 5.717 | 7.692 | 7.313 |
| P. E. $_\sigma$.......... | ± .106 | ± .133 | ± .093 |
| C. V............... | 12.979 | 19.928 | 17.775 |
| P. E. $_V$........... | ± .241 | ± .345 | ± .225 |

### TABLE F.

CONSTANTS OF RAYS FOR 1900, 1903, AND THEIR SUM.

|  | 1900 | 1903 | Combined |
|---|---|---|---|
| Number............. | 658 | 757 | 1415 |
| Mean............... | 28.038 | 25.247 | 26.545 |
| P. E. $_M$........... | ± .107 | ± .122 | ± .086 |
| Modes, empirical.... | 27, 31, 33 | 16, 22, 26, 33 | 16, 22, 26, 31, 33 |
| $\sigma$................ | 4.070 | 4.990 | 4.792 |
| P. E. $_\sigma$........... | ± .076 | ± .087 | ± .061 |
| C. V............... | 14.516 | 19.764 | 18.052 |
| P. E. $_V$........... | ± .270 | ± .344 | ± .229 |

florets, together with the two partial curves of which each is composed, are shown in *figs. 11, 12,* and *13.* These curves are all reduced to the same area, 500 units, in order to facilitate comparison, and the method of "loaded ordinates" is used to allow the curves to be superposed.

The bracts for the two years combined present no less than seven empirical modes, showing without question that 1415 heads is still too few for material having so wide a range and so high standard deviation. In the rays, the range being less and the standard devia-
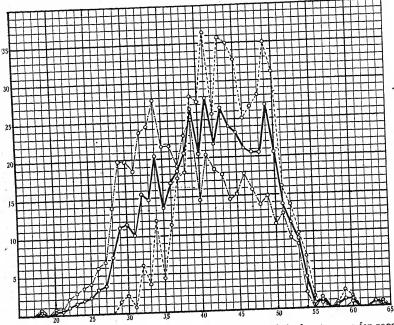


FIG. 11.—Summation curve for bracts 1900 + 1903 and the bract-curves for 1900 and 1903 superposed for comparison; all reduced to the same area, 500 units; heavy line the summation curve; dotted line the 1900 curve; dot and dash line the 1903 curve.

TABLE G.

CONSTANTS OF DISK-FLORETS FOR 1900, 1903, AND THEIR SUM.

|  | 1900 | 1903 | Combined |
|---|---|---|---|
| Number............ | 658 | 757 | 1415 |
| Mean............. | 50.298 | 44.933 | 47.428 |
| P. E. ᴍ............ | ±.166 | ±.238 | ±.156 |
| Modes, empirical.... | { 48–49, <br> { 52–53 | { 38–39, <br> { 44–45, <br> { 50–51, <br> { 56–57, <br> { 64–65 | 49–50 |
| σ................ | 6.310 | 9.703 | 8.724 |
| P. E.σ............ | ±.117 | ±.168 | ±.111 |
| C. V.............. | 12.546 | 21.595 | 18.395 |
| P. E.ᴠ............ | ±.233 | ±.374 | ±.233 |

tion only two-thirds as great, the number of heads is much more . nearly adequate.   There are presented five empirical modes, 16, 22, 26, 31, 33, almost in agreement with LUDWIG'S series.

5. *Correlations.*—The correlation between rays and bracts is shown in *fig. 14*, between rays and disk-florets in *fig. 15*, and between
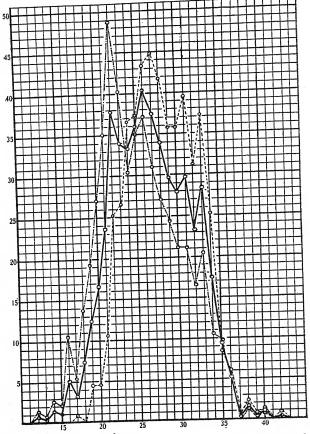


FIG. 12.—Summation curve for rays 1900 + 1903 and the ray-curves for 1900 and 1903 superposed for comparison; all reduced to the same area, 500 units; heavy line the summation curve; dotted line the 1900 curve; dot and dash line the 1903 curve.

bracts and disk-florets in *fig. 16*.   The coefficient of correlation is very high in all, being greatest between rays and bracts, and least between rays and disk-florets.   The coefficients may be compared with those of 1900 in Table H:
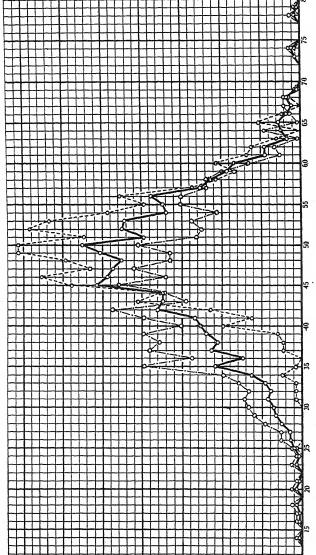
FIG. 13.—Summation curve for disk-florets 1900+1903 and the disk-floret curves for 1900 and 1903 superposed for comparison; all reduced to the same area, 500 units; heavy line the summation curve; dotted line the 1900 curve; dot and dash line the 1903 curve.

FIG. 14.—Correlation surface for 757 heads collected in 1903; rays subject, bracts relative; $\rho = .8745 \pm .0042$.

TABLE H.

COEFFICIENTS OF CORRELATION.
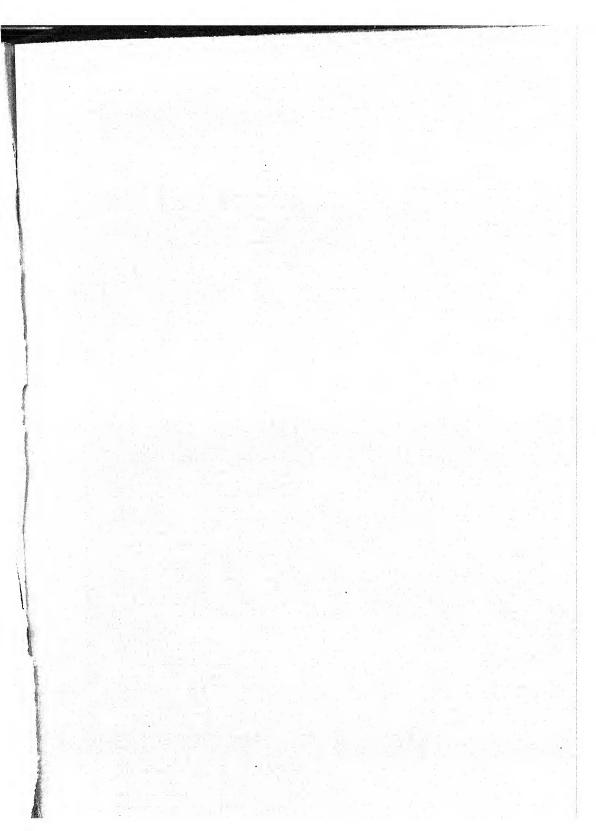
| | 1900 | 1903 |
|---|---|---|
| Rays and bracts............. | .7051 ± .0092 | .8745 ± .0042 |
| Rays and disk-florets........ | .6749 ± .0100 | .8240 ± .0058 |
| Bracts and disk-florets....... | ............ | .8355 ± .0055 |
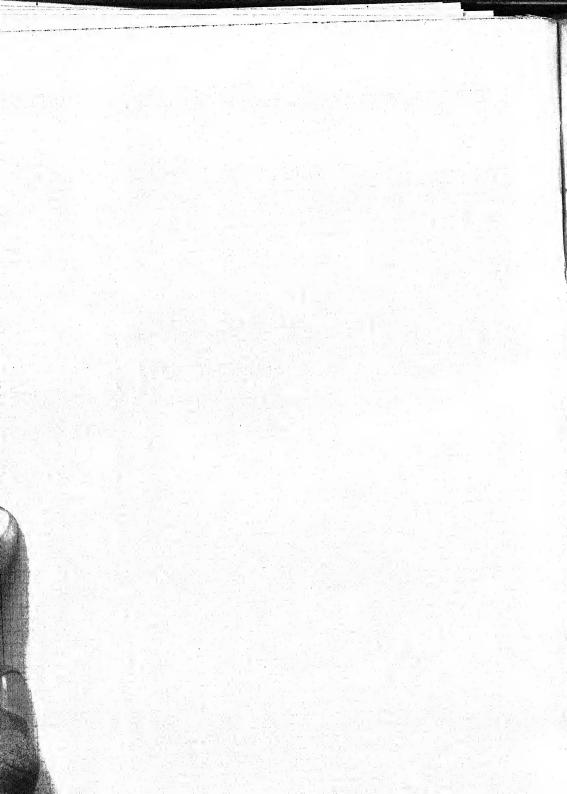
## V.  DISCUSSION.

In my earlier study the conclusion was reached that the mean number of parts in the heads of *Aster prenanthoides* begins high and falls continuously from the beginning to the end of the flowering season. This was recognized as in accord with Burkill's (1895) results on *Alsine media* and other species. Reinöhl (1903) has recently made a very careful study of *Alsine media* and reports that the first flowers never have the highest number of stamens and that the maximum number is reached only after some time. He attributes Burkill's results to the fact that they were based upon occasional collections which, he supposes, did not happen to involve the very earliest flowers of the season. My collections of *Aster prenanthoides* in 1900 included all the heads which bloomed that year, but the first collection was made so late that the mean numbers of parts in the very earliest heads were indeterminable because of their association with heads of later development; but in 1903 the collections were made with such frequency as more closely to analyze the changes taking place during the season, there being presented here twelve successive collections instead of four.

It is now shown that in *Aster prenanthoides* also the mean numbers begin low, leaping almost immediately to the maximum, and thence falling more gradually till near the end of the season. Inspection of *fig. 7* will make it clear that four collections in 1903, made on the same dates as the 1900 collections, would have led to the conclusions then reached that there is a continuous fall from the beginning to the end of the season.

It will be noted in the same figure that the last collection in 1903 shows a rise in mean values. As this collection consisted of but four heads, it can be considered as having little significance. I believe, however, that this condition will be found to occur not infrequently.

It was observed by BURKILL (1902) in *Ranunculus arvensis* L., but he did not "feel justified in suggesting a cause for it." BURKILL (1895) showed in his earlier paper that in *Caltha palustris, Ranunculus arvensis*, and *R. bulbosus* the first flower of any individual has a higher number of stamens than any subsequent flower of that individual. HAACKE (1896) points out the same fact in regard to the number of rays in the heads of *Tanacetum (Chrysanthemum) corymbosum*. If this is also true in *Aster prenanthoides* (and I believe it is), how are we to account for the peculiarities of the curves in *fig.7*? The general fall in mean values from near the beginning to near the end of the flowering period can be best explained perhaps by the gradual waning of vegetative vigor during the time at which the differentiation takes place which determines the number of parts in the heads. This decreasing vigor was supposed by BURKILL (1895) to be largely due to changing temperature, but REINÖHL (1903) has shown that temperature has little if any influence, while the important factor seems to him to be that of available food-supply. It is conceivable that there may be a decreasing lability of the protoplasm resulting from lessened water-supply, or the accumulation of inert products of metabolism, or from other causes, which would bring about a progressive fall in the number of parts in the heads, even though the food-supply remained unchanged.

But if every individual produces the highest number of parts in the first head that blooms and the lowest number of parts in the last, how can the mean number begin low—far below the maximum—and end with a rise? This is to be explained by the fact that we are dealing with a population instead of an individual. The precocious flowering of starved or otherwise weakened individuals is a well-known phenomenon, and it is evident that the heads gathered at the first collection were those produced by the very weakest individuals, and owe their low values to that fact. Very soon, however, the mediocre plants, composing the great majority of the population, begin to bloom, thus bringing the mean values at once to the maximum, from which they gradually fall until almost the end of the season. The very last to bloom will undoubtedly be the last heads of certain very vigorous individuals which did not begin to bloom till late in the season, and though these heads have the lowest numbers of parts produced

by those individuals, they yet have higher numbers than the last heads of the mediocre portion of the population which determined the minimum mean value. These facts will be made clear by a reference to *fig. 17*, in which the numerous oblique parallel lines represent the change in mean number of parts in the heads of the individual stems composing the population. The abscissal distances of the ends of a given line indicate the time at which the individual represented by that line began to bloom and that at which it ceased blooming, while the ordinatal distances of the same points represent the number of parts in the first and last heads produced. The heavy line running through the middle of the figure is the exact mean of the figure as drawn. This figure is somewhat schematic, of course, but it is not wholly imaginary. The



Fig. 17.—Schematized representation of the changes in mean number of parts in the heads of the 1903 population; each of the parallel oblique lines represents the change in a single stem; the heavy line shows the change in mean value for the whole population.

mean is suggested by the 1903 bract-curve of *fig. 7*, and the outline will be recognized in the distribution of numbers in Table A, which also belongs to the bracts of the 1903 population, so that *fig. 17* may be looked upon as a slightly schematized representation of the bracts as they actually occurred in 1903.

In 1900 the change in mean values from the maximum to the minimum was 11.6 per cent. in bracts, 14.4 per cent. in rays, and 18.9 per cent. in disk-florets; and in 1903 it was 24.6 per cent. in bracts, 22.3 per cent. in rays, and 26.4 per cent. in disk-florets. This con-

siderable change in the constants of variable characters during the single season is now generally recognized, as has been made manifest in the discussions which were roused by LUDWIG's (1901) interpretation of such differences as indicative of the establishment of local races or *petites espèces*. Miss LEE (1902) says in her discussion of LUDWIG's results and conclusions, " we require in fact to know how the means, variabilities, and correlations of the characters of a plant change (i) with its season and (ii) with the influence of environment before we can formulate a test for racial differences," and PEARSON (1903) and other recent writers make similar statements.

While there is thus a general recognition of the changes which may be expected to take place during a single season, there is still a question as to changes of variability from season to season. This is the first investigation in which factors involved in modifying the variable characters of plants or animals have been so completely limited to the dissimilarity of different seasons. Although a number of students have at times found differences similar to those presented in this paper, their material has been collected nearly always in such a way as to allow of some other interpretation, and the conclusions arrived at have in consequence usually assumed the absence of seasonal fluctuations.

YULE (1902) has investigated the number of sepals of *Anemone nemorosa* growing in several different habitats in the neighborhood of Bookham, Surrey, England, during the years 1889–1900, but unfortunately his collections were not made at coincident dates of the several years, and one of the habitats had changed during the time in which the observations were made from an exposed clearing to a well-grown shady copse. Although he interprets his results as indicating a considerable fluctuation from season to season, his data can be thrown into a single series and shown to exhibit just the changes which recent investigations of REINÖHL (1903) on *Alsine media* and the results recorded here for *Aster prenanthoides* show to occur during a single season. Thus, taking YULE's data for habitat (C), which he describes as a narrow strip of copse at Little Bookham, and arranging them according to the time of year at which each collection was made, without regard to the year, we have for the mean number of sepals: April 8–12, 1899, 6.63; April 15,

1900, 6.81; April 21–22, 1898, 6.76; May 7, 1898, 6.51. A comparison of these results with the curves in *fig. 7* will show them to be strictly comparable with the conditions exhibited by *Aster prenanthoides* in the single season of 1903. They differ, however, in being much less striking, the greatest change of mean value in *Anemone nemorosa* being only 4.4 per cent., while the greatest change in mean value in *Aster prenanthoides* was 26.4 per cent.

The Clifton area of *Aster prenanthoides* is in a perfectly natural condition, and though the region is much visited for its fine scenery, this particular spot, being less attractive to tourists and at the same time more difficult of access, is not likely to be at any time seriously disturbed. It can be assumed with perfect assurance that there were no appreciable differences in the habitat in the two years 1900 and 1903, except such as were due to meteorological differences, and to these factors or possibly to internal periodicity, or a combination of these internal causes and climatic changes must be attributed the great differences found.

It has not been infrequent to find great differences in variable characters of plants from markedly different habitats, as in the daisies (*Chrysanthemum Leucanthemum* and *C. segetum*) collected from barren hills and fertile valleys by LUDWIG and DE VRIES. But here at Clifton, Ohio, in the same spot, in the very same group of plants, undoubtedly consisting largely of the uniparental offspring of the very same individuals, the mean number of bracts was nearly 12.4 per cent. less in 1903 than in 1900, the mean number of rays was nearly 10 per cent. less, and the mean number of disk-florets 10.6 per cent. less.

If such differences as these are due to climatic fluctuations, it is of interest to consider what factors may have been important in producing them. As already mentioned, REINÖHL (1903) considers the chief factor in determining the number of parts in the androecium of *Alsine media* to be the condition of the available food-supply, whether this be dependent upon the character of the soil or upon photosynthetic activity conditioned by the intensity of the light. As the physical and chemical conditions of the soil in the Clifton ravine were doubtless essentially the same in the two years in question, the only soil factor which need be taken into account is water-supply as influenced by precipitation. REINÖHL (1903) states that he could
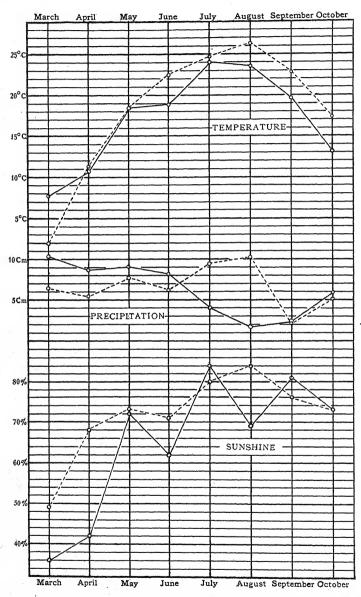
Fig. 18.—Comparison of the climatic conditions during the growing season of 1900 and 1903; dotted lines for 1900; unbroken lines for 1903; temperature curves represent conditions at Dayton, Ohio; precipitation curves are for Cedarville, Ohio; and the sunshine curves for Cincinnati, Ohio.

observe no influence produced by differences of temperature other than that of acceleration or retardation, but as conditions of nutrition are greatly affected by temperature, it is conceivable that it may be in some cases an important factor in determining variability. On these considerations I have sought to compare the season of 1903 with that of 1900 with respect to temperature, precipitation, and light. As the U. S. Weather Bureau records are not complete for any of these factors at Clifton, I have compared the conditions at the nearest stations at which complete records were available. In *fig. 18* these comparisons are represented graphically, the temperature-curves representing conditions at Dayton, Ohio, about 60 $^{km}$ distant, the precipitation-curves made from data for Cedarville, Ohio, 10 $^{km}$ distant, and the curves for light-intensity from the self-recording instrument at Cincinnati, Ohio, 160 $^{km}$ distant. These data are tabulated in Tables I, K, and L, along with the eleven-year or twelve-year normal, and such fragmentary data as were attainable for Clifton itself.

As this is the first attempt to refer changes in the variability of plants in a state of nature to definite climatic changes, there are obvious difficulties in the way of making satisfactory interpretations, and these difficulties can be overcome only by further study. We need to know (*a*) the relative importance of the several factors involved, (*b*) the harmonic optimum of each climatic factor for the species in question, (*c*) whether the critical period is that which precedes or that which accompanies differentiation, (*d*) the time of beginning and ending of the period of differentiation.

TABLE I.

TEMPERATURE IN DEGREES CENTIGRADE.

| | DAYTON, O. | | | CLIFTON, O. | |
|---|---|---|---|---|---|
| | 1900 | 1903 | 11-yr. normal | 1900 | 1903 |
| March................. | 2.0 | 7.7 | 4.3 | .... | 8.9 |
| April................. | 11.3 | 10.7 | 11.3 | 10.3 | 10.6 |
| May.................. | 18.4 | 18.4 | 17.4 | 18.0 | 17.9 |
| June................. | 22.4 | 18.9 | 22.6 | .... | 17.9 |
| July................. | 24.7 | 24.0 | 24.8 | 24.3 | 23.0 |
| August............... | 26.2 | 23.5 | 23.0 | 25.1 | 22.6 |
| September............ | 22.7 | 19.7 | 19.5 | .... | .... |
| October.............. | 17.2 | 13.1 | 12.6 | .... | 13.1 |

### TABLE K.

PRECIPITATION IN CENTIMETERS.

| | CEDARVILLE, O. | | | CLIFTON, O. | |
| --- | --- | --- | --- | --- | --- |
| | 1900 | 1903 | 11-yr. normal | 1900 | 1903 |
| March................ | 6.45 | 10.41 | 10.14 | .... | 7.98 |
| April................. | 5.51 | 8.79 | 5.87 | 4.83 | 8.51 |
| May.................. | 7.70 | 9.07 | 8.71 | 5.00 | 11.58 |
| June................. | 6.20 | 8.20 | 8.18 | .... | 11.94 |
| July................. | 9.32 | 4.11 | 9.63 | 13.05 | 3.05 |
| August............... | 10.29 | 1.75 | 5.54 | 9.04 | .79 |
| September............ | 2.08 | 2.46 | 5.74 | .... | .... |
| October.............. | 5.11 | 5.92 | 4.67 | .... | 5.77 |

### TABLE L.

LIGHT-INTENSITY AT CINCINNATI, OHIO.

| | 1900 | 1903 | 12-yr. normal |
| --- | --- | --- | --- |
| March............. | 49% | 36% | 45% |
| April............. | 68 | 42 | 56 |
| May............... | 73 | 72 | 62 |
| June.............. | 71 | 62 | 72 |
| July.............. | 80 | 84 | 76 |
| August............ | 84 | 69 | 75 |
| September......... | 76 | 81 | 72 |
| October........... | 73 | 73 | .. |

No study has been made to determine the period of differentiation in *Aster prenanthoides*, but I am assured by Dr. C. J. CHAMBERLAIN, who has studied *Aster Novae-Angliae*, that some of the heads in that species are already blocked out by the first of July. I consider it a fair assumption that the period of differentiation of the parts of the head in this species lies between June 1 and August 1.

If we accept the normal climatic conditions as near the harmonic optima (and this may not be a very erroneous assumption, since the area in question is near the center of range), we find that the conditions were more favorable in 1900 (*a*) with respect to June and July temperatures, the temperature for these months in 1903 being considerably below normal, (*b*) in July precipitation, 1903 having less than half the normal precipitation for that month, and (*c*) in light-intensity for every month, except possibly May, up to August 1, after which no factor could have any further influence. It may well be a question,

however, whether the harmonic optimum for light-intensity is not likely to be above the normal, the shade habit of *Aster prenanthoides*, as well as of other green shade plants, being assumed on account of the protection afforded against excessive transpiration, and not against excessive lighting. If this be true, the conditions in 1900 were even more favorable than here assumed, since with the exception of July the light-intensity was higher in 1900 than in 1903, being generally above normal in the former year, while in 1903 it was generally much below normal, being strikingly below in April and June.

These several advantages of 1900 over 1903 seem to be offset by the single factor of precipitation during May and June, the rainfall being appreciably below normal during those two months of 1900. As pointed out in the discussion of the habitat, it is probable that precipitation is of very slight importance in this case, leaving the low light-intensity and low temperature of the month of June, 1903, as probably the most important factors in bringing about the great change in the number of parts in the heads, the factors of next importance being possibly the very high light-intensity coupled with slight precipitation in the month of July 1903.

I wish to repeat that these conclusions are based on assumptions which need confirmation. It must not be forgotten that the after-effects of a preceding season or a rigorous winter may also be factors of importance, or even that there may be an internal periodicity which cannot be definitely referred to environmental fluctuations.

Two features of the frequency polygons for the bracts, rays, and disk-florets (*figs. 8–10*) are sufficiently striking to warrant consideration, their multimodality and their skewness. So much has been written upon the multimodal character of the frequency curves of phyllotactic organs that it need only be pointed out here that this additional collection of material shows no tendency to eliminate the multimodality observed in 1900, and though the errors of random sampling, which are very great in material of such wide range, must be held to account for most, if not all, of the irregularities of these curves (PEARSON 1902), there are some evidences that permanent modes may be developed on the Fibonacci series and LUDWIG'S "Unterzählen."

The constant recurrence of this series is not to be taken, however,

as has been maintained by LUDWIG (1899, 1901), as proof that
variation in plants is fundamentally different from that in animals.
When the phyllotactic series shall have been successfully analyzed,
they may be found to result from the working out of more or less
definite cell-lineages as supposed by LUDWIG (1888), or they may be
the result of purely mechanical relations, as believed by SCHWEN-
DENER, followed by WEISSE (1897) and CHURCH (1904), but either
hypothesis, in explaining the occurrence of such series, must leave
departures from the theoretical numbers to be accounted for as
fluctuating variations. In addition to this variation about each num-
ber of the series, there is the general variation which may have a
sufficiently wide range to allow the variates to coincide with two or
more numbers of the phyllotactic series, so that we have in the case
of phyllotactic variants two series of variations, the one overlying and
partially masking the other. There can be little doubt that these
variations taken separately will be found to agree with all the laws of
variation determined for animals and the non-phyllotactic characters
of plants.

Although DE VRIES (1899b) was able by selection to establish
races of *Chrysanthemum segetum* having monomodal ray-curves, this
must not be taken as supporting LUDWIG'S (1901) view that multi-
modality is due to the establishment of a mixed population of *petites
espèces* through the common occurrence of asexual and autogamic
sexual reproduction, for REINÖHL (1903) was able to reduce the
multimodal curves of *Alsine media* to monodal curves *without selec-
tion*, by different degrees of light and manuring.

It is to be hoped that we shall soon have a method of treatment of
phyllotactic variants which will remove the Fibonacci mask and
permit the analysis of the underlying individual variation with as
much precision as is now attained with non-phyllotactic variants.

Although it is impossible on account of the multimodality of these
curves to analyze the skewness, it is so marked in the case of the bracts
and rays (*figs. 8* and *9*) as to be recognized at a glance. There have
been various interpretations of skewness in different connections,
favorite early views (DAVENPORT 1901) being that it results either
by the elimination of one or other of the extremes through the
process of natural selection, or that heterogeneity is introduced by the

development of a new race within the range of the old but centering about a different mean. It is also believed that skewness may result from physiological causes having no direct bearing upon the origin or modification of species. While in no specific case may the suggested interpretation be the correct one, these different views may at least be accepted as evidence that skewness may result from various causes, and that it is therefore not self-explanatory.

If the 1903 curves are compared with those for 1900 in *figs. 11–13*, it will be seen that in every case the positive sides of the curves are approximately coincident, but on the negative side there is a very material disagreement. According to the recent discussion of skew variation by LUTZ (1904), we have here a case of skewness produced by the addition of variates, and this addition of such magnitude as already to overtop the 1900 population, thus giving a fine example of "historic" skewness; but no one can be convinced that this is here due to the "starting of a new race about a mean within the range of the old race."

It is evident that the skewness is here the result of direct physiological reaction to the changed environment. Not all individuals are alike sensitive to changed conditions, some being more, some less affected by a given amount of change; so that while many individuals respond to the less favorable conditions by the production of heads with smaller numbers of parts, there is still a considerable number of conservative individuals which are little or not at all affected. The positive skewness of these curves is due to the fact that only a small proportion of the population is conservative. If the great mass of variates had been comparatively conservative and only a small percentage sensitive to the changed conditions, it is plain that the position of the principal modes would have been little affected, while the mean would have been lowered and negative skewness would have been the result. This would then have been a case of so-called "prophetic" skewness. We may say then that in cases of direct or physiological variation, prophetic skewness indicates slight sensitiveness, and historic skewness great sensitiveness,[5] to the changed conditions, provided always, of course, that under ordinary conditions the distribution of the variates affected is normal.

[5] As measured by the number of sensitive individuals, not by the degree of sensitiveness of each individual.

Cases are well known in which the distribution does not appear to be normal under any ordinary conditions, the frequency curves being of the "half Galton" type, as for instance the petals of *Caltha palustris*, *Potentilla anserina*, *Ranunculus bulbosus* (DE VRIES 1894), *Ranunculus repens* (PLEDGE 1897), sepals and petals of *Ranunculus arvensis* (BURKILL 1902), leaflets of clover (DE VRIES 1899*a*), ascidia and other abnormalities of various species (DE VRIES 1899*a*, TAMMES 1903), and other characters. Such cases may not be really so exceptional, however, as they at first appear. We have only to assume that the normal condition for these characters is one in which the value of $\sigma$ approaches zero to see that these are cases of "prophetic" skewness due to the small proportion of abmodal variates; in other words, due to slight sensitiveness to conditions tending to produce a number of organs higher or lower than the normal mode.

It may be found that any population or even any species is sufficiently uniform in its reactions to various degrees of environmental change to allow us to derive from the direction and amount of skewness the approximate value of the mean under average conditions or under conditions which would give a normal distribution of the variates. Thus, the knowledge that this population of *Aster prenanthoides* is so sensitive to change as to exhibit strong positive skewness when conditions are below average may be found to warrant the assumption that there will be a strong negative skewness under unusually favorable conditions, and also that the skewness exhibited by a collection from any new locality would give an indication by its direction as to whether that collection was below or above the average prevailing condition for that place. But before we can apply this principle with any confidence in determining the "normal mean" of any particular population, it will be necessary to confirm our assumptions (*a*) that the distribution for that population is normal under average conditions, and (*b*) that the sensitiveness to unusually favorable conditions is similar in intensity to the sensitiveness to unfavorable conditions.

The principle here presented of variability in individual sensitiveness to changes of environment is likely to find a wide applicability in the interpretation of skew variation, and suggests the need of first determining whether or not there is direct variation of the organ or

character under consideration before assuming that either natural selection or mutation is involved in any given case of skewness. And although this is most strikingly true of plants, it must likewise be true of animals, especially of animals having a short life-cycle, so that no investigation can be considered as giving satisfactory support to any hypothesis of evolution until the sensitiveness of the character under consideration to secular changes shall have been determined.

Perhaps even more remarkable than the skewness and the changes in mean value, which have resulted from the less favorable conditions in 1903, is the great increase in value of the coefficient of variability. Reference to Tables E, F, and G will show that the variability in the bracts in 1900 was $12.979 \pm .241$, as compared with $19.928 \pm .345$ in 1903. Corresponding changes are shown in rays and disk-florets, from $14.516 \pm .270$ to $19.766 \pm .343$, and from $12.546 \pm .233$ to $21.595 \pm .374$, respectively. As it has been assumed that the low mean values indicate that conditions were less favorable in 1903 than in 1900, we may accept these changes in the coefficients of variability as proof of the hypothesis that when organisms are introduced into unusual surroundings or subjected to unusual conditions they become more variable, and that this would be favorable to any selective process which might set in as a result of the change. Before too great stress is laid on this conclusion, however, we need to consider the nature of the coefficient of variability. The importance of this constant lies in the fact that it is an abstract number and therefore allows us to compare the variability in characters of different magnitude or even of different quality, as color, form, size, weight, number, etc. It consists of two factors, the standard deviation ($\sigma$) and the mean ($M$), and is expressed by the formula $C.\,V. = \dfrac{100\,\sigma}{M}$. The value of the coefficient of variability will change directly with changes of $\sigma$ and inversely with changes of the mean. Turning now to the cause of the greatly increased coefficient of variability, we find upon inspecting Tables E, F, and G that the value of $\sigma$ was in every case considerably higher in 1903 than in 1900, and at the same time that the mean was much lower, so that both factors acted together in producing the high values of the coefficient of variability.

To show that this coefficient is not always a satisfactory measure

of variability, let us assume that conditions had been unusually favorable to such a degree as to give curves with the same values of $\sigma$, but negatively skew. The variability would then be approximately the same, but, instead of the coefficient being the same or even nearly the same, it would be very much less, owing to the greatly increased value of the mean. I do not think that $\frac{100\,\sigma}{M}$ gives a proper value of the coefficient of variability in cases of skew variation, since its values in positively skew curves are not comparable with those in curves of the same species or even of the same population, which are negatively skew. If the "normal mean" could be derived from skew curves, that might be used instead of the mean in the formula for the coefficient of variability, thus making the value of $\sigma$ alone indicate the changes of variability from time to time within one and the same population. This would be theoretically correct, but it must be evident that the experimental determination of the normal mean, except through a long series of investigations upon any population under consideration, is impossible, even though, as pointed out above, the degree and direction of skewness may in some cases give a rough approximation to it when the sensitiveness of the species in question is known.

Returning now to the question as to the increased variability due to changed environmental conditions, we find that the present imperfect coefficient of variability, which would tend to minimize the variability when conditions are unusually favorable, would still be considerably increased by such unusually favorable conditions as would result in a negative skewness equal in magnitude to the positive skewness of the 1903 curves. We may confidently accept the results of this study as proof, therefore, that changes of environment do result in increased variability.

It was noted in 1900 that the correlations between the parts in the head were very high, and by reference to Table H it will be seen that in 1903 they were very considerably higher still, the highest coefficient in both years being that between bracts and rays. The exact meaning of changes in the degree of organic correlation is proving a somewhat puzzling problem at the present time. LUDWIG (1901) presents a striking case of this kind as evidence of racial distinctness between

two populations of *Ranunculus ficaria*, but MacLeod (1899) has shown that similar changes may be found in that species at different times in a single season. I have also found (Shull 1902) that the coefficients of correlation in *Aster prenanthoides* may be very different at different parts of the season.

Before the significance of such changes can be understood it will be necessary to investigate the nature of correlation when considered in this statistical way. Some biologists use the term "correlation" to designate a relation between two organs or characters, such that the development of the one determines that of the other, as for instance the dependence of the secondary sexual characters upon the primary in animals, or the relation of the internodes to the leaves in plants. In this kind of correlation the failure of the one organ or character to develop, or its removal at an early stage of development, invariably prevents or modifies the development of the other. Every degree of correlation in this sense is found in different cases, and it probably exists to some extent even between organs whose immediate relations to each other are little understood. It is only rarely, however, that this kind of correlation is not insignificant as compared with biometrical correlation. Thus, in the biometrical sense there is a very high correlation between the index fingers of the right and left hands, but the removal of one of these would have no appreciable effect upon the development of the other.

For convenience we may speak of "immediate" or "direct" correlation when one organ or character stands in a direct causal relation to another, and "mediate" or "indirect" correlation in cases of correlated variation in which no such direct dependence exists. Statistical measures of correlation make no distinction between these two kinds of correlation, but as a notable degree of immediate correlation is comparatively rare, while mediate correlation is almost universal, the correlation of parts as spoken of by the biometrician may be considered as mediate or indirect. Mediate correlation between two organs or characters may be defined, then, as their mutual relation to the combination of common causes, such as heredity, nutrition, etc., which determine their quantitative relations. It is the relation which results in proportion and symmetry. When mediate correlation is perfect, *i. e.*, when $\rho = 1$, the two organs or

characters are proportionately influenced by every variation in the factors which determine their size, number, or other quantitative relation, and neither is affected by any factor which does not affect the other. The organs do not modify each other, but both are affected by the same conditions. Only confusion results from the failure to appreciate the difference between immediate and mediate correlation, as may be seen in BURKILL'S (1902) discussion of the correlation in the parts of the flower of *Ranunculus arvensis*, when he says that "reduction in the number of petals does not act as a reflex on the number of sepals in anything like the way in which the reduction of sepals may be said to promote reduction of petals."

If as the values of any pair of mediately correlated organs or characters are increased or decreased the correlation between them is changed, it must mean that one or other of them becomes proportionately less sensitive to the causes producing the change of values, and becomes more fixed or more variable in its quantitative relations. Such a change is well illustrated by an interesting diagram presented by BURKILL (1902), in which it is shown that sepals, petals, stamens, and carpels of *Ranunculus arvensis* vary together, *i. e.*, are closely correlated, in flowers having the total number of parts less than 19, but in flowers having a higher total number of parts the sepals become fixed in number at 5, and the correlation between sepals and the parts which continue to increase becomes zero. In flowers with more than 22 parts the mean number of petals likewise becomes fixed at 5. In flowers of still higher numbers of parts the carpels show a tendency to respond with proportionately less increase as compared with the stamens. It is plain then that in this species any conditions which promote the formation of flowers with a high number of parts will tend to decrease the degree of correlation and *vice versa*.

But it is an important fact which must not be overlooked that changes in the *coefficient* of correlation do not necessarily mean an actual change in correlation. PEARSON (1903) has pointed out that heterogeneity in a population tends to increase the coefficient of correlation, but of course such heterogeneity does not increase the actual degree of correlation. It is probable that most of the marked changes which have thus far been observed in coefficients of correla-

tion are to be accounted for in this way. I have already shown that my first collection in 1900 was made long after the beginning of the flowering season, and hence had the earliest heads with low numbers of parts associated with the heads having the highest numbers of parts produced during the season, and this fact sufficiently explains the high correlations found in that collection. A similar explanation may account for the considerable increase in the coefficients of correlation between the parts of the heads in 1903 as compared with those of 1900, as there are associated in the 1903 collection the heads of conservative individuals and those of individuals which were much modified because of their great sensitiveness to the unfavorable conditions in the latter year. It is apparent, therefore, that in cases of changed coefficients of correlation, as in other cases, it is necessary to scrutinize carefully the influence of more or less artificial conditions upon the value of the constants before we can appreciate their biological significance

The results of this study have fully borne out the suggestion that considerable differences may occur in individual variation from year to year, and it shows that such differences may be even greater than one would expect. It is not likely that this is an extreme case, nor that the differences between these two collections is even near the limit for this species. To some these results may seem to preclude the possibility of deriving anything of further value from quantitative studies of variation, while to others many new problems of great interest and importance will be suggested. The interpretations which students have based upon the assumption that seasonal fluctuations do not occur will have to be greatly revised or discarded altogether, and before we can appreciate the exact bearing of any case of variation upon the great problems of evolution it will be necessary to know the laws governing that variation. It is to problems of this nature that students must direct their earnest attention if we are ever to have a basis for the appreciation of the bearing of individual variation.

## VI. SUMMARY.

A second collection of heads of *Aster prenanthoides* Muhl. was made in 1903 from the same area at Clifton, Ohio, that supplied material for a quantitative study in 1900. The bracts, rays, and

disk-florets were studied quantitatively, and the results compared with those of the earlier study.

Twelve successive collections were made from the same plot, and it was found that the earliest collection had low mean numbers, that the mean values then leaped quickly to a maximum, falling gradually to near the end of the season, and that the last collection exhibited a rise, the rise in mean values at the beginning and at the end of the season being in disagreement with the conclusion reached in my earlier study. In general, the first head to bloom on any stem has the highest number of parts possessed by any head produced by that stem, and the last to bloom has the lowest number. The low mean numbers at the beginning of the season are due to the precocious flowering of the weakest individuals, and similarly the rise at the end of the season is due to the belated flowering of a few very vigorous individuals.

Comparison of the results with those of 1900 show that the mean values in 1903 were 10–12 per cent. lower than in 1900, and that accompanying these low mean values there are a strong positive skewing of the curves, a remarkable rise in the coefficient of variability, and a considerable increase in the coefficient of correlation.

The difference in the mean values for the two years is attributed to less favorable climatic conditions in 1903, chiefly to low temperature and low light-intensity in the month of June.

The skewness is due to the unequal sensitiveness of individuals to changes of environment. It is positive because the proportion of conservative individuals is small. In direct or physiological variation, "historic" skewness indicates great sensitiveness and "prophetic" skewness indicates slight sensitiveness to the changes of environment.

The great increase in the coefficient of variability is due to an increase in the standard deviation and a decrease of the mean. The present coefficient of variability is not satisfactory in cases of skew variation, and the value of $\sigma$ alone should be used as the measure of changes of variability in one and the same population.

Changes in the coefficient of correlation may be due either to an actual change of correlation or to the introduction of a greater or less degree of heterogeneity. The latter is probably responsible for the changes noted in this species.

I gratefully acknowledge my indebtedness to Dr. C. B. DAVEN-PORT, under the inspiration of whose lectures this study was under-taken, and under whose direction it was largely carried on; to Miss OLIVE D. COE for the care with which the material was collected, for the negatives from which *figs. 1, 4,* and *5* were reproduced, and for the original of *fig. 6;* to the Directors of the U. S. Weather Bureau stations at Columbus, Ohio, and at Cincinnati, Ohio, for climato-logical data; and to the curators of numerous public and private herbaria for the data upon which *fig. 3* is based.

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# BRIEFER ARTICLES.

## A NEW SHEEP-POISON FROM MEXICO.

THROUGH the kindness of Professor ALFRED DUGÈS of Guanajuato, Mexico, I have recently had an opportunity to examine specimens of a plant, locally known as *moradillo*, which occurs on the Hacienda de Santiago in Zacatecas, Mexico. This plant is said to poison sheep which eat it. From its floral structure, as well as its habit, there can be no doubt that it belongs to the small solanaceous genus Bouchetia. Only two species of this genus are recognized as valid, namely *B. erecta* DC. and *B. procumbens* DC., both published by DUNAL in De Candolle's *Prodromus* **13**[1]: 589. 1852. Of these, *B. erecta*[1] is a well-known much-branched erect or decumbent plant, 7 to 30 cm high, growing in rocky thickets, etc., of the southwestern United States, Mexico, and southward to Argentina. The corolla is 14 to 18 mm long, being about twice the length of the calyx. The proper tube of the corolla is short and entirely included within the calyx. The habit of the plant is closely that of an Evolvulus. *B. procumbens* is a very poorly known species, founded upon one of the drawings of the Mociño and Sesse collections. The tracing of this drawing (Calques des Dessins, *pl. 920*) shows a plant with a cluster of five slightly thickened roots. From the united summit of these spring eight leafy strongly decumbent or perhaps prostrate stems. These are in some cases as much as 12 cm long. The leaves have the narrow lanceolate or oblanceolate form prevalent in *B. erecta*, but the corolla has a slender considerably exserted proper tube. The limb is represented as about 1 cm broad, the lobes being subacute or even shortly acuminate.

So far as I know, the only specimen ever referred to this species since its description was a part of Schaffner's no. 611 from the Valley of San Luis Potosi, a plant so determined by Mr. W. B. HEMSLEY (Biol. Cent.-Am. Bot. **2**:437). This plant (in herb. Kew) I have not seen. Mr. HEMSLEY also mentions some specimens (Schaffner's no. 69 and Parry & Palmer's no. 701, from San Luis Potosi, as well as Graham's no. 270 from Jalapa)

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[1] The synonymy of this species is as follows: *Nierembergia anomala* Miers, Ill. S. Am. Pl. **1**:99. *pl. 20.* 1846. *N. staticaefolia* Sendt. in Mart. Fl. Bras. **10**:179. 1846. *Bouchetia erecta* DC. acc. to Dunal in DC. Prodr. **13**[1]:589. 1852. *Leucanthea Roemeriana* Scheele, Linnaea **25**:258–259. 1852. *Bouchetia anomala* Britton & Rusby, Trans. N. Y. Acad. Sci. **7**:12. 1887.

which he doubtfully refers to a variety of *B. procumbens* with "floribus quam in icone fere duplo majoribus." Of the numbers here mentioned, Dr. Schaffner's nò. 69 and Parry & Palmer's no. 701 are in the Gray Herbarium and appear identical with the sheep-poisoning plant recently sent by Professor DuGÈS. The stems are very short (3 to 4 ᶜᵐ in length) and prostrate; they spread from the summits of a 2–several-branched caudex. The flowers, mostly appearing terminal, are more than 3 ᶜᵐ long and 2 ᶜᵐ in diameter, the long slender proper tube of the corolla greatly exceeding the calyx. The lobes of the corolla are rounded or retuse. I cannot at all believe that this is the plant sketched in the Calques des Dessins, *pl. 920*, which has the grumose roots, far longer branches, narrower corolla-limb and pointed lobes. It seems best, therefore, to characterize the large-flowered plant as a new species. The name chosen alludes to its baneful effects on sheep.

**Bouchetia arniatera,** n. sp.—Perennis pilis albis minutis curvatis non-glanduliferis subcanescens: caudicis erectis vel patentis ramis subterraneis saepe elongatis flexuosis pallidis; caulibus aeriis pluribus brevibus 3–4 ᶜᵐ longis prostratis foliosis prope apicem florentibus: foliis lanceolatis vel elliptico-oblanceolatis 8–11 ᵐᵐ longis 2.5–4 ᵐᵐ latis breviter petiolatis acutis vel obtusiusculis uninerviis: pedunculis 3–6 ᵐᵐ longis teretibus; floribus solitariis: calycis lobis lanceolatis obtusiusculis erectis 4 ᵐᵐ longis quam tubus ovato-turbinatus paulo longioribus: corollae purpureae 32–35ᵐᵐ longae 2 ᶜᵐ latae externe obscure glanduloso-puberulae tubo proprio gracili e calyce longe exserto, faucibus gradatim ampliatis, limbi lobis ovato-deltoideis apice rotundato vel retuso: filamentis equalibus paulo sub media parte corollae affixis filiformibus glabris 11 ᵐᵐ longis; antheris crassis ovoide's 1.5 ᵐᵐ longis: capsula ovoidea obtusiuscula 6 ᵐᵐ longa: seminibus 1 ᵐᵐ longis pallide brunneis irregulariter ovoideis, integumento externo sub laxe celluloso.—*B. procumbens*, var.? Hemsl. Biol. Cent.-Am. Bot. **2**:437. 1882.—In mountains of San Miguelita, Valley of San Luis Potosi, August, 1876, *Dr. J. G. Schaffner*,[2] no. 69 (hb. Gray), distributed as Petunia; San Luis Potosi, 1878, *Drs. Parry & Palmer*, no. 701

[2] The form of Schaffner's name here given is the one used on his printed Latin labels. Dr. Schaffner was a German apothecary, a native of Darmstadt; who settled in Mexico and collected extensively in the neighborhood of the city of Mexico, Orizaba, and San Luis Potosi. He signed himself in two ways, sometimes as Wilhelm Schaffner sometimes as J. G. Schaffner. The two signatures have given rise to some confusion and a question as to the identity of the person or persons concerned. The "G" doubtless stands for the Latin Guilielmus and the "J" probably for Johann or Johannes. This first initial, in the manner of the Germans being regarded as relatively unimportant, was dropped by Schaffner in his ordinary German signature.

(hb. Gray); Hacienda de Santiago, Zacatecas, communicated by *Prof. A. Dugès*, June, 1904 (hb. Gray).

The reported poisonous qualities of *B. arniatera* certainly raise a suspicion regarding the nearly related *B. erecta*, which is frequent in some grazing regions of our southwestern states where, in case of unexplained sheep-poisoning, it would be well for veterinarians to investigate the toxic effects of this plant.—B. L. Robinson, *Gray Herbarium.*

## SOME WESTERN SPECIES OF AGROPYRON.

**Agropyron spicatum Vaseyi** (Scribn. & Smith), n. comb.—*A. Vaseyi* Scribn. & Smith, U. S. Dept. Agr., Div. Agros., Bull. 4:27. 1897.

After a careful study of a large series of specimens I am disposed to regard *A. Vaseyi* as a depauperate form of *A. spicatum.*

**Agropyron subvillosum** (Hook.), n. comb.—*Triticum repens subvillosum* Hook. Fl. Bor.-Am. 2:254. 1840. *A. dasystachyum subvillosum* (Hook.) Scribn. & Smith. U. S. Dept. Agr., Div. Agros., Bull. 4:33. 1897.

Much field study of this grass has led me to regard it as a distinct species. With its slender culms and small spikelets it is certainly quite different in appearance from the stouter and larger-flowered *A. dasystachyum* and *A. occidentale.* Often it is not at all glaucous, but quite green, and the flowering glumes are sometimes merely scabrous. It is very common in this region, occurring on bench-lands and alkali flats.

**Agropyron Bakeri**, n. sp.—A smooth cespitose perennial, with stout culms, 3–5 $^{dm}$ high: leaves rigid, flat, prominently striate-nerved; culm leaves three, 12–20 $^{cm}$ long, 2–4 $^{mm}$ wide, those of the innovations longer: spike 9–12 $^{cm}$ long, scarcely exserted, equaled or exceeded by the uppermost leaf; spikelets terete, 5–9 $^{mm}$ distant, 5-flowered, 15–19 $^{mm}$ long: empty glumes 11–12 $^{mm}$ long, two-thirds the length of the spikelets, 5-nerved (the nerves scabrous), margins scarious, narrowly oblong, somewhat abruptly narrowed into an awn 2–8 $^{mm}$ long, and with or without a tooth to one side at the base of the awn: flowering glumes scabrous or nearly smooth on the back, the strong midnerve extended into a rigid widely spreading awn 10–35 $^{mm}$ long, often bidentate below the origin of the awn: palea equaling or somewhat exceeding its glume: rachilla scabrous.

Related to *A. violaceum* and *A. Gmelini*, but distinguished by its stout culms, firm and strongly nerved leaves, and long widely spreading awns. Type specimen in the Rocky Mountain Herbarium, collected by C. F. Baker, no. 139, near Pagosa Peak in southern Colorado, altitude 2750 $^{m}$ (9000 feet), August, 1899.—Elias Nelson, *University of Wyoming, Laramie.*

## NOTE ON SOME BRITISH COLUMBIAN DWARF TREES.

(WITH THREE FIGURES)

WHILE at the Minnesota Seaside Station on the west coast of Vancouver Island during the past summer, an interesting forest of dwarf trees was discovered. For the most part they grew on the weather-worn edges of a strongly inclined slate formation, but a few were found in crevices between blocks of diabase. They were all close to the sea, but outside the influence of the surf. Mr. F. K. BUTTERS and I succeeded in getting a number of



FIG. I.
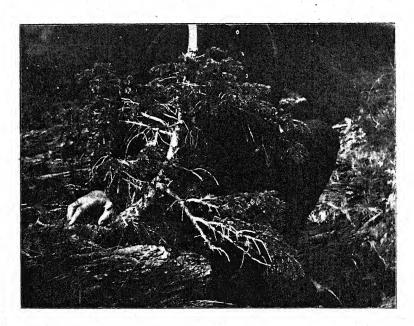
photographs, after securing which we cut down the trees and determined their age by the help of hand lenses and the compound microscope.

The dwarf trees were of three species: *Picea sitchensis*, *Tsuga heterophylla*, and *Thuja gigantea*. The pictures herewith presented, however, are all of the Sitka spruce. *Fig. 1* shows the largest tree photographed and also the youngest. It was a little less than two feet high and sixty-eight years of age. The leaf-bearing phytomeres were decidedly short, but the leaves remain upon the twigs for several years, so that he effect in the picture is of twigs o ord'nary length. *Fig. 2* shows a tree growing in a.

cleft of the diabase. It was less than a foot in height, with trunk three-quarters of an inch in diameter. It turned out to be eighty-six years old. *Fig. 3* shows a tree cut-down and held in the writer's hand. It was about a foot high, with trunk one inch in diameter, and ninety-eight years old.

These trees have very much the appearance of the well-known Japanese dwarf trees, so much so indeed that it would be an easy matter for the unscrupulous to pot them and palm them off on innocent purchasers. Their striking resemblance to the famous products of Japanese horticultural art suggested to me that from such seashore dwarfs the Japanese might very easily have obtained their hint and learned the tricks of culture.



FIG. 2.

Two strong dwarfing influences are at work upon these little British Columbian trees. In the first place, the root system is strongly compressed between plates of rock. Of some of these trees the whole root system was exposed and it looked a good deal like a sheet of brown paper with the trunk of the tree attached to one edge. In the second place, the winds from the sea dwarf and contort the twigs. So with great pressure upon the root system and strong wind action upon the shoot the dwarfing is accomplished.

These little trees have a very different appearance from the slender dwarf spruces of bogs in northern Minnesota. In such regions trees with trunks an inch or so in diameter have been noted, showing an age up to sixty years, but they are tall, slender, and regular in the arrangement

of their branches.  The dwarf trees of mountain tops have likewise a decidedly different appearance, so far as they have come within my observation, and do not particularly resemble the Japanese products.

I do not remember to have seen it suggested anywhere that the dwarf
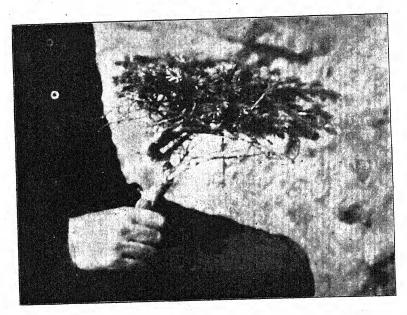


FIG. 3.

trees of Japan are essentially of seashore origin, but in view of the little natural forest on the coast of Vancouver, I think it very possible that this is a correct explanation.—CONWAY MACMILLAN, *University of Minnesota, Minneapolis.*

## CELLOIDIN TECHNIQUE: A REPLY.

IN THE August number of the GAZETTE, Dr. CHARLES J. CHAMBERLAIN publishes a criticism of a recent contribution by Mr. A. B. PLOWMAN on the subject of celloidin imbedding.  As the account of the method was written up by Mr. PLOWMAN at my suggestion, and the "Correction" of Dr. CHAMBERLAIN contains several misconceptions, I think it well to publish a short reply.  Dr. CHAMBERLAIN is unable to find anything new in the method beyond the preliminary use of hydrofluoric acid.  If so accomplished a technician takes the trouble to reperuse the article in question,

he will discover, in the very careful removal of air from the tissues before imbedding, the numerous accurately graded solutions of celloidin (2, 4, 6, 8, etc., per cent.), the repeated heating and rapid cooling of the objects during the process of infiltration, the thickening of the final matrix by the addition of chips of celloidin and the use of heat (instead of the usual process of evaporation), the hardening by means of chloroform followed by STRASBURGER'S solution of equal parts of alcohol and glycerin, the method of attaching the objects to the microtome, etc., etc., features of greater or less novelty in celloidin technique. It is scarcely necessary to discuss the misconception on the part of Dr. CHAMBERLAIN, by which he supposes Mr. PLOWMAN to claim originality in the matter of using celloidin as an imbedding medium. The reference to previous incomplete accounts was perhaps unfortunate, but was due to the fact that Mr. C. H. MILLER, an assistant in the Anatomical Department of the University of Chicago had described imperfectly the celloidin method at present under discussion as derived from Prof. R. R. BENSLEY, a former colleague of the present writer. In his chapter on celloidin technique, Dr. CHAMBERLAIN too makes reference to his indebtedness to Mr. W. B. MAC CALLUM, a former student of the Ontario Agricultural College, an institution into which the present writer's celloidin method had certainly been introduced. The writer is glad to accept Dr. CHAMBERLAIN's statement, in a letter to Mr. PLOWMAN, that he owes nothing to Dr. MAC CALLUM. The mention of possible prior publication arising out of the wide informal diffusion of the method was not introduced out of any desire to establish priority, but for the purpose of obviating just such well meant criticisms as that of Dr. CHAMBERLAIN. The excuse for publishing the method is the fact that it gives results which excel those obtained by any other process known to the writer.—E. C. JEFFREY, *Phanerogamic Laboratories of Harvard University.*

THE correction to which Professor JEFFREY refers in his reply was based upon the following data:

Celloidin in 2, 4, 6, 8, 10, and 12 per cent. solution is mentioned in LEE'S *Vade Mecum* (ed. 3, 1893, pp. 193–195). The series in multiples of two seems due to the fact that the SCHERING's celloidin, which is most commonly used, comes in tablets accompanied by directions stating that a 2 per cent. solution may be made by adding to a tablet a sufficient quantity of ether-alcohol to make the whole weigh 2000$^{gm}$. For a 4 per cent. solution another tablet could be added, and so on. The chloroform method for hardening celloidin after infiltration was described by VIALLANES in 1883 (Rech. sur l'hist. et le dével. des insects, p. 129; also Revue scientifique **31**: 684–687.

1883).  A mixture of equal parts of glycerin and alcohol was recommended by STRASBURGER (Das botanische Practicum 1884, p. 79) for facilitating the cutting of woody tissues.  EYCLESHYMER (Amer. Naturalist **34**: 354–357. 1892, and Jour. Roy. Micr. Soc. **1892**: 563–565) describes a series of four grades of celloidin for infiltrating, chloroform for hardening, and a treatment with glycerin before cutting.  In view of these facts, we do not doubt that others, who like ourselves have used STRASBURGER's method for softening woody tissues, have continued to use the glycerin and alcohol mixture when dealing with material imbedded in celloidin.

Mr. PLOWMAN has certainly presented the subject in a very usable form, and in perfecting the application of fluoric acid he has made it possible to obtain better sections of refractory tissues.  In my "correction" I intended merely to lodge an objection to the characterization of my account as a second-hand presentation of Dr. JEFFREY's methods.  A study of LEE's *Vade Mecum* and the references there cited indicates that Dr. JEFFREY, like myself, is deeply indebted to previous investigators.—CHARLES J. CHAMBERLAIN.

I HAVE been permitted to read the proof of Dr. CHAMBERLAIN's comment on my letter.  Matters have now resolved themselves into a difference of opinion between Dr. CHAMBERLAIN and myself as to what constitutes novelty and improvement in celloidin technique.  I am very willing to allow the case to rest on the practical value of the method published by Mr. PLOWMAN.—E. C. JEFFREY.

## AN ABNORMAL AMBROSIA.

### (WITH THREE FIGURES)

A PLANT of *Ambrosia artemisiaefolia* that had been run over by a wagon and badly injured bore both staminate and pistillate flowers in an abnormal condition.  The young shoots bearing the flowers arose vertically from the prostrate and injured main stem.

The staminate flowers of this injured plant appeared larger than the normal.  The heads were scattered, forming a loose raceme, and each contained fewer flowers than usual.  In the center of the older flower heads there was a group of buds that appeared to be vegetative (*fig. 1*), while the younger heads contained vegetative buds only within the bracts enclosing the heads, the flowers having been entirely replaced.  Instead of the sterile style the older staminate flowers bore vegetative buds in the center (*fig. 2*).  The pollen of these flowers appears to have been arrested

in development. In some cases the grains were shriveled and not well formed, in other cases the pollen seemed to have been checked just beyond the tetrad stage.

The pistillate flowers of the same plant bore no ovules, but instead of them there were small vegetative buds (*fig. 3*). These flowers were not clustered as usual, but were mostly in the axils of leaf-like bracts, for the most part being considerably separated and forming a very loose raceme. The styles were glandular at tip only. In tracing the development, the bud appeared very early replacing the ovule, and the parts of the flower were more lengthened. A rudimentary ring-like outgrowth appeared just beneath the carpel, corresponding to the corolla of the staminate flower (*fig. 3, p*).
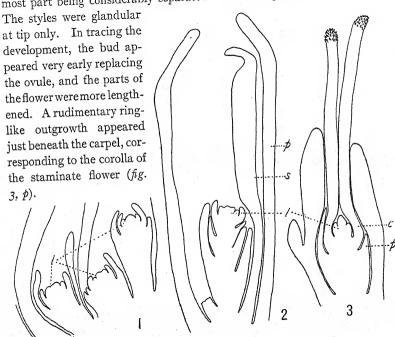


FIG. 1.—Vegetative buds (*l*) in the center of a staminate head.
FIG. 2.—A vegetative bud (*l*) replacing the sterile style; *s*, stamen; *p*, corolla.
FIG. 3.—A vegetative bud (*l*) replacing the ovule; *c*, carpel; *p*, corolla.

All the staminate flowers examined had styles more or less rudimentary. In some of the marginal flowers the styles protruded beyond the corolla and were terminated by a disk fringed by glandular hairs. Ovules were not formed in any specimen, but a tissue that had the appearance of a rudimentary ovule was seen in some flowers.

It would appear that under the abnormal conditions described the primordia that usually form reproductive parts produced vegetative parts.
—A. C. Life, *Shaw School of Botany, St. Louis, Mo.*

# CURRENT LITERATURE.

## BOOK REVIEWS.

### The adaptation theory.

FROM THE time of LAMARCK the theory of direct adaptation to environment has found its adherents, and there certainly appear to be many facts which are best explained by some such theory. Dr. CARL DETTO, assistant at the Botanical Institute of the University of Jena, has made a careful reinvestigation of the subject, in the light of the most modern botanical knowledge.[1] The first chapters deal with methodological postulates and a general statement of the problem of adaptation. It is evident from the first sentences that the author is radically opposed to the Lamarckian theories and especially to the Neolamarckian aspect of those theories as held, for example, by Wettstein. It is to be feared that DETTO sometimes loses the appearance of impartiality, and becomes a partisan, anxious to maintain his view at all hazards. He regards the capacity for an advantageous response to new and hitherto unexperienced conditions as the central feature of Lamarckism, and thinks that the most refined Neolamarckian views are of a kind with the more coarse and obviously teleological expressions of LAMARCK and NÄGELI. He believes that those who hold to direct adaptation are necessarily teleologists and vitalists, and fundamentally in error because they attempt to explain physical phenomena by means of psychological data. The presence within an organism of a capacity for an advantageous response to changed conditions is called an ecologism, while the development of an advantageous from an indifferent state is called ecogenesis. The difficulty with Lamarckism is that it takes the ecologism for granted; a true explanatory theory will have to explain how it came into existence, i. e., we are in need of a theory to account for ecogenesis.

DETTO examines the evidence that has been adduced in support of direct adaptation, especial consideration being given to "accommodation" or "regulation," as exhibited by bacteria, molds, the biological species among the Uredineae, and the "xerophytic," "hygrophytic," and "hydrophytic adaptations" among vascular plants. Many changes usually regarded as advantageous, which ensue when aerial organs are placed in water, are here referred to hypoplasy, and it is held that the reduced or modified structures may be of slight benefit or even no benefit at all. Other changes may be due to reversion, or to the removal of the cause of arrest. The chief recourse of the author, however, is to what he terms the

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[1] DETTO, CARL, Die Theorie der direkten Anpassung und ihre Bedeutung für das Anpassungs- und Deszendenzproblem. Versuch einer methodologischen Kritik des Erklärungprinzipes und der botanischen Tatsachen des Lamarckismus. 8vo. pp. vi +214. Jena: Gustav Fischer. 1904. M 4.

potential limit of variation; the supposed direct adaptation is in reality nothing new, but rather the manifestation or release of a hitherto latent property. The new habitat is merely empirically new. Consequently DETTO agrees with KLEBS that a species should not be defined as it exists normally in nature, but should include all possible variations in all imaginable conditions. The capacity of an organism is not widened but demonstrated by environmental changes. Direct adaptation or ecogenesis is impossible because it implies that there is a setting aside of the constitutionally prescribed effect of a given stimulus in the interest of the organism, or that menacing factors are in reality beneficial. The direct adaptationist conceives of a vital mechanism that looks out for the future, and holds advantageous reactions in readiness for conditions which have never yet occurred! Ecogenesis must therefore be indirect in all cases, chance alone determining whether the new ecologism is of advantage or not. DETTO, who agrees with KLEBS at so many points, holds in direct opposition to him that the external world causes no changes whatever in plants; every plant character is an organization character (in Nägeli's sense) and the external conditions in which a plant is placed act merely as releasing stimuli.

The book should be read carefully by all who are interested in the philosophy of adaptation, since the volume as a whole is so written as to stimulate good thinking. However, it seems to the reviewer that the perspective is frequently distorted. In this country, at least, there is no need for such a continuous and hearty lampooning of teleological and vitalistic views, for they have been long since abandoned by most scientific investigators. That chance determines success and not a prudent foresight on the part of the plant is certainly the common view. Again, if one holds to a *potentielle Variationsbreite* wide enough to embrace all changes that ever occur in plants, it is obviously impossible ever to demonstrate the contrary by experiment; it is a concept incapable of proof or disproof. It seems far better to hold that both the organism and the environment are needed to secure the evolution of new forms; any other view seems to the reviewer fundamentally unthinkable.—HENRY C. COWLES.

### Matthias Jacob Schleiden.

AN APPRECIATIVE biography of SCHLEIDEN by M. MÖBIUS, was published on the centennial of his birth, April 5, 1904.[2] MÖBIUS was related by marriage to SCHLEIDEN (whose second wife was MÖBIUS's maternal aunt), and to him family sources of information have been open. SCHLEIDEN's life was uneventful save for two incidents; the one an attempt at suicide on account of his want of success and dissatisfaction in the legal profession, and the second his resignation of the professorate at Jena because of the refutation of his theories on the origin of cells and the formation of the embryo. Clear and vigorous in thinking and expression, he demanded accuracy and lucidity in others and was ever ready to

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[2] MÖBIUS, M., Matthias Jacob Schleiden zu seinem 100 Geburtstage. 8vo. pp. iv +106, portrait, *figs. 2.* Leipzig: Wilhelm Engelmann. 1904. *M*2.50.

criticise sharply. Indeed, polemics seem to have been his delight, and he attacked without reference to the standing of his antagonist, as his famous controversy with LIEBIG shows, *à propos* of which UNGER wrote ENDLICHER: "Den arroganten Liebig hat Schleiden ganz köstlich zugedeckt."

The greater part of the book is devoted to an account of SCHLEIDEN's published work, including an account of his famous cell-theory, his classical *Grundzüge der wissenschaftlichen Botanik*, many minor papers, popular addresses and books, his editorial activity, and his philosophical, religious, and speculative writings. For many important services to the science of his day, and especially to botany, this many-sided man deserves of the present generation fuller recognition. This book, with its interesting portrait and character portrayal, will promote this and is a useful contribution to the history of botany.—C. R. B.

## MINOR NOTICES.

ENGLER [3] has published a new edition of his *Syllabus*, including the most recent results of his views as to relationships. This complete outline of his classification, including as it does the whole plant kingdom, is of great service to students of morphology as well as of taxonomy. There is a prefatory statement of the principles of this particular scheme of classification, and an appendix containing the geographical regions recognized by the author.—J. M. C.

WILLOUGHBY, Vermont, has long been famous for its flora, and KENNEDY [4] has done good service in publishing a compact account of the region and a list of 690 plants. The characteristic features of the region are wet cliffs and slides and sphagnous cedar swamps. The small area in which the species are massed is remarkable, probably nine-tenths of the indigenous species being found in two square miles.—J. M. C.

COULTER and DORNER [5] have published a simple key to the genera of the forest trees of Indiana, using the most obvious characters. Its practical value in large classes has led to its publication, and its usefulness is not restricted to Indiana.—J. M. C.

CRATTY [6] has published a list of the vascular plants growing in Emmet county, Iowa, a northwestern county bordering on Minnesota. The list includes 590 numbers.—J. M. C.

[3] ENGLER, A., Syllabus der Pflanzenfamilien. Eine Uebersicht über das gesamte Pflanzensystem, etc. Vierte, umgearbeitete Auflage. 8vo. pp. xxx+237. Berlin: Gebrüder Borntraeger. 1904. *M*4.

[4] KENNEDY, GEORGE G., Flora of Willoughby, Vermont. Reprinted from Rhodora **6**: 93–134. *pls. 54–56.* 1904.

[5] COULTER, STANLEY, and DORNER, H. B., A key to the genera of the forest trees of Indiana, based chiefly upon leaf characters. 16mo. pp. 12. Lafayette, Indiana: published by the authors. 1904.

[6] CRATTY, R. I., Flora of Emmet county, Iowa. A list of the native and introduced plants. Reprinted from Proc. Iowa Acad. Sci. **11**: 201–251. 1904.

## NOTES FOR STUDENTS.

YABE [7] gives his opinion that COVILLE's ericaceous genus Arcterica,[8] from Bering Island, is *Pieris nana* Makino, common on the higher peaks in Honshu and Hokkaido, Japan. The plant was originally described as *Andromeda nana* Maxim., of which genus Pieris is often regarded as a section.—J. M. C.

HOLM [9] has been investigating the inflorescence of Cyperus, chiefly with reference to the prophylla. It is claimed that by means of the "cladoprophyllon" the originally erect and congested rays of the umbel are brought to their more or less horizontal position. Also, the small bodies always observable at the base of the secondary branches of the inflorescence of grasses, more distinct in large panicles, are said to represent rudimentary prophylla identical with those characteristic of the Cyperaceae.—J. M. C.

FUJII [10] in a short preliminary announcement gives the results of his investigations upon the droplet which exudes from the micropyle of gymnosperms at the time of pollination. The preliminary announcement deals with *Taxus baccata.* Chemical tests indicate that the droplet contains glucose and calcium. A kind of gum and perhaps also malic acid are present. SCHUMANN claimed that only one droplet is produced. The present investigation shows that droplets may be formed repeatedly, both in the laboratory and in the field.—CHARLES J. CHAMBERLAIN.

VERSCHAFFELT [11] finds that the minimum lethal strength of some toxic solutions for fleshy or succulent organs of potato, Aloe, Rheum, etc. can be determined with fair accuracy by noting the change in weight which occurs when the test object is removed from the toxic solution and immersed in water. The basis of the method is that tissues which have succumbed to toxic exposure lose in weight by yielding osmotically held water, or at least do not gain in weight by water absorption as compared with controls. The method has limitations, some of which are noted by the author.—RAYMOND H. POND.

THE EXPERIMENTS upon which Elfving based his theory of positive and negative galvanotropism have been repeated by PLOWMAN [12] with results for the most part confirmatory. Two exceptions to be noted are, first, that an electric

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[7] YABE, Y., On a new genus Arcterica. Bot. Mag. Tokyo **18**: 127–128. 1904. Abstract.

[8] See BOT. GAZ. **37**: 298–302. 1904.

[9] HOLM, THEO., Studies in the Cyperaceae. XXIII. The inflorescence of Cyperus in North America. Am. Jour. Sci. IV. **18**: 301–307. 1904.

[10] FUJII, K., Ueber die Bestäubungstropfen der Gymnospermen. Vorläufige Mitteilung. Ber. Deutsch. Bot. Gesells. **21**: 211–217. 1903.

[11] VERSCHAFFELT, E., Determination of the action of poisons on plants. Konin. Akad. Wetens. Amsterdam **1904**: 703–707.

[12] PLOWMAN, A. B., Electrotropism of roots. Amer. Journ. Sci. IV. **18**: 228–236. *pls. 9–10.* 1904.

current passing through water in which seedlings are growing is not necessarily fatal, and that the roots of such seedlings will curve toward the positive pole even when the current is of less than lethal strength; second, that negative galvanotropism is not a constant property of any species thus far studied. Since electrons instead of ions are the cause of the curve responses the author proposes to substitute for Elfving's "galvanotropism" the term "electrotropism."—RAYMOND H. POND.

NEWCOMBE [13] reports experiments on thigmotropism of terrestrial roots which show very feeble sensitiveness of the terminal millimeter and of the growing region, the few responses being positive and the angle of deviation small. Many ingenious modes of securing continuous pressure and avoiding hydrotropic stimuli as far as possible were tried. The most convincing results were gained by surrounding roots with collapsible collodion tubes, and using a water stream to give the pressure. The tubes do not allow appreciable filtration. These experiments gave strong evidence for the identity of rheotropism and thigmotropism, and NEWCOMBE applies to thigmotropism the results given by his earlier experiments on rheotropism.[14] The sensitiveness is equal on all sides, and the stimulation must extend over a considerable area and be continued for some time to produce a complete reaction. The feeble sensitiveness is probably of no utility to the plant.—C. R. B.

BRANDT holds [15] that REINKE errs in thinking the N-content of the sea small [16] because little is added to it. His estimates of the yearly addition of organic N-compounds and of inorganic N-compounds by rains would indicate an N-content in sea water that analysis does not corroborate. This discrepancy is explained by the active dentrification through the action of bacteria, so that the N-content never surpasses a minute amount. This dentrification has been shown to occur and the bacteria have been carefully studied in several localities in the North Sea, the East Sea, and even in the Antarctic under the ice. It is the chief reason for the smaller N-content of tropical waters and this difference determines the lesser amount of plant life there. BRANDT believes the N-supply quite adequate without special appeal to such bacterial symbionts as Clostridium and Azotobacter, though these insofar as they occur may be effective. For example, in the water of Kiel Bay (at 20$^m$) the content in inorganic N is four times that of the plankton.—C. R. B.

[13] NEWCOMBE, F. C., Thigmotropism of terrestrial roots. Beihefte Bot. Cent. **17**:61–84. 1904.

[14] BOT. GAZ. **33**: 183. 1902.

[15] BRANDT, K., Ueber die Bedeutung der Stickstoffverbindungen für die Production im Meere. Beihefte Bot. Cent. **16**: 383–402. 1904.

[16] REINKE, J., Die zur Ernährung der Meeres-Organismen disponiblen Quellen an Stickstoff. Ber. Deutsch. Bot. Gesells. **21**: 371–380. 1903. See BOT. GAZ. **37**: 228. 1904.

PILOSTYLES is a genus of the Rafflesiaceae parasitic upon various Leguminosae. Material from Brazil has been studied by ENDRISS [17] in GOEBEL's laboratory. The staminate flower consists of a solid axis in which are imbedded two circles of sporangia, with 18–20 sporangia in each circle, twenty being probably the usual number. If four sporangia represent one anther, the whole structure would represent five anthers, corresponding in some measure to the relations obtaining in the ovulate flower, which has normally five placentae. While the flowers are monosporangiate, a rudiment of the ovary appears as a column in the center of the staminate flower. In related forms the flowers are said to arise endogenously, within an originally compact tissue. In *Pilostyles Ingae* the flowers are strictly exogenous. The pollen grains are extremely small, measuring only $5\,\mu$ in diameter. Some flowers have been pollinated, but in only one case had pollen tubes begun to form. Many older seeds contained embryos, but no trace of pollen or pollen tubes could be found. The writer doubts whether normal fertilization occurs. The anatomy of the plant and the development of the embryo are described.—CHARLES J. CHAMBERLAIN.

VARIOUS ATTEMPTS have been made to attribute to external conditions the polarity seen in cuttings of roots and shoots. The latest effort is by KÜSTER, who discusses in a preliminary paper [18] the influence of oxygen and of centrifugal force upon polarity, and in a second [19] enlarges upon the same topic. KÜSTER placed the roots of Taraxacum, which under uniform conditions of moisture produce roots at the apical (normally lower) end and shoots at the basal end, with their basal (normally upper) ends in water and the opposite ends pointing upwards into the air. Shoots develop on the latter end and none on the parts in water. Cuttings of the stems of *Ribes aureum* placed with their basal ends in water and their apical ends in moist air produced roots only on their apical ends. *Salix vitellina* gave similar results, showing a marked tendency for the roots to appear only where there is a sufficient supply of air. Cuttings of Salix and other plants were rotated horizontally on a centrifuge. The centrifugal force acted as a check upon development, the inhibition being in proportion to the force, *i. e.*, if the apical end describe the greater circle the buds there are inhibited more than those at the opposite end. In this way the usual polarity may be reversed.— W. B. MACCALLUM.

LYON [20] has made a detailed and much-needed study of the embryogeny of Ginkgo, with an unusual abundance of illustration. The general undifferentiated mass of tissue that is known to fill the egg after free nuclear division is called

[17] ENDRISS, W., Monographie von *Pilostyles Ingae* (Karst.). (*Pilostyles Ulei* Solms-Laub.)  Flora **91**: 209–236. *pl. 20. figs. 31.* 1902.

[18] KÜSTER, ERNST, Experimental Untersuchungen über Wurzel- und Sprossbildung an Stecklingen.  Ber. Deutsch. Bot. Gesells. **22**: 167–170. *pl. 1.* 1904.

[19] KÜSTER, Beiträge zur Kenntnis der Wurzel und Sprossbildung an Steckling. Jahrb. Wiss. Bot. **40**: 279–302. *figs. 4.* 1904.

[20] LYON, HAROLD L., The embryogeny of Ginkgo.  Minn. Bot. Studies **3**: 275– 290. *pls. 29–43.* 1904.

the "protocorm." The cells in the micropylar two-thirds of this spherical proto-
corm divide little or not at all, but the cells of the antipodal extremity form
a small-celled meristem which passes over directly into the meristem of the
"blastema" or "metacormal bud." The blastema invades the endosperm as a
broad, blunt cylinder, the protocormal tissue being forced back through the neck
of the archegonium, many of its cells often being crushed. The metacormal
bud is meristematic throughout, but soon two "growth-foci," those of stem and
root, are organized in its axis and very close together. Later the primordia of
the two cotyledons are organized in the marginal region of the broad apical
meristem. Thus in the organization of the embryo much of the original proto-
cormal tissue is not involved, heretofore being described as a rudimentary sus-
pensor. There are usually two cotyledons, but in certain of the material three
cotyledons were quite common; they are normally equal and entire, and spring
apart when liberated from the seed. The anatomy of the embryo, including
its histogenesis, is also described.—J. M. C.

BESSEY has studied the effect of various external factors on the pigment
formation in several fusarium-like fungi.[21] The plants used were (1) two fungi,
closely resembling each other, isolated from the roots of diseased sesamum plants,
(2) *Neocosmospora vasinfecta* and (3) its variety *nivea*, and (4) *Fusarium cul-
morum*. Of these the first four when grown on acid media produce a red pigment
which changes to dark blue when treated with alkalies. The fungi were grown in
KNOP's solution to which the substances to be tested were added. No general
relation could be established between the composition of the culture medium
and the production of pigment. Mono-, di-, tri-, and polysaccharides generally
gave a red or violet pigment, which changed to blue in cases where the culture
became alkaline during the experiment (gelose). Organic acids gave a scarlet
color, except palmitic acid which is not soluble. Salts of the acids with few excep-
tions gave no pigment. In alkaline media no pigment production takes place.
Absence of air also suppresses the development of the coloring matter. These
fungi also produce a yellow pigment whose formation is independent of the char-
acter of the substratum. Light and oxygen are necessary for its production.
The pigments are formed in the cells of the fungi and not primarily in the sub-
stratum as has been stated.—H. HASSELBRING.

SHIBATA's [22] mycological studies of endotrophic mycorhizas in Podocarpus,
Psilotum, Alnus, and Myrica have given the following results: In the tubercles
of Podocarpus the mycelium of the fungus develops extensively, and is then
digested and resorbed by the cells of the host. The nucleus of the infected cell
divides repeatedly amitotically, the nuclei increasing greatly in staining capacity

[21] BESSEY, Ernst A., Ueber die Bedingungen der Farbbildung bei Fusarium.
Flora **93**: 301–334. 1904.

[22] SHIBATA, K., Cytologische Studien über die endotrophen Mykorrhizen. Jahrb.
Wiss. Bot. **37**:643–684. *pls. 14–15.* 1902.

on account of the increase in a nuclein-like material. After the digestion of the fungus the nuclei of the host cells resume their normal appearance. The increase and subsequent decrease in the nuclein-like material indicates that the nucleus takes part in the formation of enzymes. The amitotic division is not an indication of degeneration, but is rather a means of increasing more rapidly the nuclear material. After the fungus has been digested, mitotic division is often seen in the multinucleate cells, showing that nuclei after dividing amitotically may again divide by mitosis. The number and arrangement of the chromosomes does not seem to be affected by the previous amitotic division. In Psilotum the cells containing the fungus can be distinguished as host cells and digesting cells. The nuclear change consists chiefly in a great increase in the chromatin. The formation of transverse walls in the intracellular hyphae is almost entirely suppressed. In Alnus the fungus is not a true hyphomycete. A plasmatic body appears in the nucleus of the infected cell, and within the body are numerous droplets which disappear after digestion of the fungus has been completed. The fungus in Myrica belongs to the genus Actinomyces, the first instance of actinomycosis recorded.

In all the mycorhizas studied the cytological changes are intimately connected with the intracellular digestion of the fungus substance. The presence of a typical digestive fluid was established in all cases. The mode of nutrition of the endotrophic fungus is still an open question.—CHARLES J. CHAMBERLAIN.

AMAR [23] has recorded data obtained from histological and physiological study of the rôle of calcium oxalate in plant nutrition. As a general rule the root contains few if any crystals, and they become less numerous as one follows the course of foods from the leaf blade to the root. Crystal formation in the leaf is localized chiefly in tissues adjacent to those concerned with photosynthesis and conduction. The crystals represent excreted waste and not reserve products in storage. AMAR seeks to relate the formation of oxalate crystals to physiological conditions resulting from the chemical composition of the nourishment absorbed, but in the opinion of the reviewer he does not present convincing evidence. He found that each species has a minimum requirement for Ca, up to which crystals do not form, and above which they form in proportion as the Ca exceeds the minimum requirement. Since crystals do not form in seedlings grown without any calcium, the author attributes the retarded growth in such cases to deficiency of this element, and concludes that the crystals form under natural conditions to reduce the excess of calcium rather than to remove oxalic acid from solution. The justification for this conclusion is not apparent, because the experiment as tried does not exclude the presence of oxalic acid as a possible factor. In the opinion of the reviewer an important fact has been overlooked, namely that a molecule of oxalic acid consisting of just two carboxyl groups requires only the addition of one atom of oxygen for complete oxidation to carbon dioxid and water. For this reason an abnormal excretion of oxalic acid in animal metabolism has

[23] AMAR, MAXIME, Sur le rôle de l'oxalate de calcium dans la nutrition des végétaux. Ann. Sci. Nat. Bot. VIII. **19**: 197–292. *figs. 34.* 1904.

always been regarded as evidence of incomplete oxidation.   Since calcium oxalate occurs in fungi as well as in green plants, it is quite possible that oxalic acid means incomplete oxidation for plants as well as for animals.   The author's experiment would then be interpreted thus: an excess of calcium retards oxidation and hence favors oxalic acid formation; rather than that oxalic acid is formed especially to remove excess of lime.—RAYMOND H. POND.

TOBLER [24] experimented at the Zoological Station of Naples upon fragments of living Rhodophyceae taken from the detritus zone of the bay.   He finds motion essential to keep the thallus of some algae intact.   *Griffithsia Schousboei*, for instance, grew well upon a shaking machine, but fell to pieces in a day when kept quiet.   Bornetia, which normally has straight branches, only the claw-like branches about the fruiting organs being hyponastic, in darkness developed such branches at the tip of the plant.   Lack of light produces abnormal growth and other effects.   For example, alternately branched forms in the dark became oppositely branched, and oppositely branched species became whorled.   Terminal cells of *Antithamnion plumula* became elongated, lighter colored, and hair-like. Callithamnion lived three and one half months in complete darkness—longer than it had ever been cultivated in light.   Dasya grew more luxuriantly in yellow light.   About ten cells from the tip of the axis intercalary growth was induced. Etiolation phenomena represent only a general form of reaction, because cultures of a number of algae in the light show typical etiolation, which the author calls phenomena of degeneration.   Intercalary growth may occur normally in Pleonosporium and its relatives, yet it is more common in cultures placed in the light. After eight to fourteen days in darkness every cell of the axis not rarely began to form cross walls.   Later, intercalary growth occurred in the large branches also. Adventive sprouts and rhizoid-like branches are common characteristics of degeneration.   The cortex, which is an important taxonomic feature in many red algae, was found to be variable.   Pleonosporium, which has no cortex in nature, developed one in the dark.   The youngest cells of Griffithsia often fell off singly in darkness, and in darkness or in yellow light Bornetia fell into filaments or separate cells.   Such isolated cells or cell complexes may bud and develop new plants. In contrast to these forms, *Callithamnion granulatum* often cast off young cells which never formed proliferations, but quickly died.   The author explains this peculiarity by the intimate correlation between the cells of Callithamnion, which makes it impossible for them to become separated and remain alive.—ETOILE B. SIMONS.

THE ATTITUDE of experimental morphologists of the present day is decidedly toward a causal explanation for the behavior of organisms, as opposed to the teleological view of the past.   REINKE,[25] in a lengthy discussion, strenuously

[24] TOBLER, F., Ueber Eigenwachsthum der Zelle und Pflanzenform.   Versuche und Studien an Meeresalgen.   Jahrb. Wiss. Bot. **39**: 527–577.  *pl. 10.*  1903.

[25] REINKE, J., Ueber Deformation von Pflanzen durch äussere Einflüsse.   Bot. Zeit. **62**[1]: 81–112.  *pl. 4.*  1904.

opposes this point of view and argues for a "final" (which he makes synonymous with teleological) explanation. REINKE cites as illustrations upon which his argument is based the behavior of *Nuphar luteum* and *Ranunculus aquatilis* which in flowing water produce no floating leaves or flowers, of *Euphorbia Cyparissias* whose shoots are distorted by a rust fungus, and of *Lentinus lepideus* which in darkness develops a branching non-fruiting form. These cases he considers as undoubted malformations because they are forced departures from the normal type. In Nuphar, for example, the form developed in still water is "abnormal," though it always occurs under these conditions. This character, REINKE claims, not being "normal" is not hereditary; only the capability of reaction to this stimulus is hereditary. One is tempted to ask here, what is the "normal" form of this plant but evidence of its capability of reaction to the conditions of still water?

The branched non-fruiting form of Lentinus occurring in the absence of light REINKE discusses at length, and claims it to be a true malformation because it is the result of abnormal conditions, while the fruiting form is "normal" because it is the result of "normal" conditions, the test of normal or abnormal conditions here being very apparently whether they are the rule or the exception in nature. Such "abnormal" modifications according to REINKE all have this character, that they are not necessary for the life of the plant, and are not hereditary, but only potentially so, in that they occur only as reactions to definite stimuli, *i. e.*, the reaction ability is hereditary. When an organism responds to two different sets of stimuli by definite reactions in each case it seems to the reviewer rather futile to argue that one response is normal and the other is anything else.

KLEBS's work is freely quoted, and REINKE, as would be expected, takes exactly the opposite view, maintaining that there is a definite form which the plant is striving to assume, but when certain inhibiting conditions exert their influence the morphological equilibrium is disturbed and the plant, against its innate forces, is compelled to assume another form. These external factors REINKE considers as opposed to the "normal" form, and the plant, so to speak, resists them.—W. B. MacCallum.

ITEMS OF TAXONOMIC INTEREST are as follows: K. SCHUMANN (Bot. Jahrb. **34**: 325. 1904) has described a new African genus (*Stephanostema*) of Apocynaceae, and also (*idem* 331) one (*Dolichometra*) of Rubiaceae.—W. H. BLANCHARD (Amer. Botanist **7**: 1–4. 1904) has published a new species of Rubus (blackberry), with a variety, from Vermont.—H. CHRIST (Bull. Herb. Boissier **4**: 936–951. 1904) has described new species of Hymenophyllum (**12**), Trichomanes (**2**), Cyathea (**9**), and Alsophila from Costa Rica.—P. HENNINGS (Hedwigia **43**: 353–400. 1904), in concluding his Ule's *Fungi amazonici*, has described as new genera *Saccardomyces* (Englerulaceae), *Zukaliopsis* (Perisporiaceae), *Asteropeltis* and *Phaeoscutella* (Microthyriaceae), *Metadothella* (Pseudophacidiaceae), *Cicinnobella, Diplodiopsis*, and *Septodothideopsis* (Sphaeropsidaceae), *Poropeltis, Peltistroma, Seynesiopsis*, and *Phragmopeltis* (Leptostromataceae), and *Bactridiopsis* (Tuberculariaceae).

—W. LIPSKY (Acta Hort. Petrop. **23**:1–247. *pls. 1–11.* 1904), in his second contribution to the flora of central Asia, which includes Ranunculaceae to Labiatae, besides numerous new species describes two new genera (*Kozlovia* and *Ladyginia*) of Umbelliferae.—A. A. HELLER (Muhlenbergia **1**:63–110. 1904) has brought together the species of Ribes in California, with a key, recognizing 43 species, one of which is described as new; and has also described new species of Heuchera, Sidalcea, Eriodictyon, and Orthocarpus.—E. P. BICKNELL (Torreya **4**:129–132. 1904) has described three new species of Viola from Long Island.— W. A. MURRILL (*idem* 141–142) has described a new genus (*Phylloporia*) of pore-fungi from South America.—N. L. BRITTON (*idem* 142) has described a new species of Bradburya from Florida.—E. L. GREENE (Leaflets **1**:49–64. 1904) has read the riddle of NACKER's genera of Cactaceae (all of them happily synonyms); has called attention to Amarella as the proper name of the American species referred to Gentiana, describing under it eight new species; and has described seven new species of Apocynum and five new western species of Rhamnus.—ANNA MURRAY VAIL (Bull. Torr. Bot. Club **31**:457–460. *pls. 16–19.* 1904) has published two new species of Asclepias from New York and one from Kansas.—T. D. A. COCK-ERELL (*idem* 461–509. *pls. 20–23*) has published an account of the N. Am. species of Hymenoxys (formerly referred to Picradenia or Actinella), recognizing thirty species and varieties, describing eleven as new, and transferring seventeen.— J. N. ROSE (Smithsonian Miscell. Coll. **47**:159–162. *pl. 20. fig. 18.* 1904) has published a new genus (*Lenophyllum*) of Crassulaceae, comprising four species from northeastern Mexico and southern Texas.—J. M. C.

A VOLUMINOUS monograph on anthocyanin by BUSCALIONI and POLACCI [26] is in three parts. The first is a bibliography, presumably exhaustive, as it contains 866 titles, among which are Linnaeus's *Flora Lapponica* and Loudon's *Arboretum*. The industry of the authors in gathering titles has exceeded their discrimination, as the inclusion of a paper by a Mr. ROBINSON, entitled *Blue Ridge blossoms*, will testify, since it is purely a floristic list and the Blue Ridge does not owe its color to anthocyanin. The second part (114 pp.) is a critico-historical discussion of the researches of previous authors. The third part (255 pp.) contains an account of the very extensive researches of the authors, which have continued for two years. The gist of their results is here given, condensed from their own summary.

Anthocyanins appear only in highly developed plant forms. Their distribution in the parts of different plants does not accord with that of starch and indicates that they have more than one function, just as their formation depends on more than one factor. Comparative studies show that the presence of anthocyanins often involves a modification of cells. Their origin seems due to oxidases acting on sugars, glucosides, etc., while their decomposition is oftenest due to reduction. The influence of humidity, of nutrition, and of light upon them are very variable.

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[26] BUSCALIONI, LUIGI, e POLACCI, GINO, Le antocianine e loro significato biolo-gico nelle piante. Atti Istituto Botanico di Pavia II. **8**: 135–511. *pls.* 9. 1904.

They apparently tend to moderate rather than to accelerate transpiration. The relations of anthocyanins to parasitic organisms show that anthocyanic cells react against the invader by augmenting their osmotic pressure, which is accomplished by accumulating in them substances from which ultimately anthocyanins arise. Thus the pigments at once indicate and participate in the increased turgescence. Study of allogamy leads to the conclusion that floral coloration has not originated from the intervention of insects, but that the crowding of foods into the floral leaves has led first to the starvation of the chloroplasts, later to their modification, and finally to the appearance of the anthocyanic coloration, which became fixed by the agency of insects. To hold that allogamy is the primary cause of coloration seems to require belief that flowers are not only intelligent, but can voluntarily and freely alter their own bodily characteristics with varying external conditions. Finally, as the chromatic evolution of flowers is found to be probably polyphyletic, the anthocyanins can hardly have arisen from the xanthic pigments or *vice versa*. A new reagent for the anthocyanins—a solution of nicotin—is found to be the most reliable.

This monograph, which the authors call *un modesto contributo* to the study of biological problems, suffers from hypertrophy. A more careful bibliography, confined to legitimate references, a compact relation of the discordant results of previous investigators, and a condensed presentation of their own work would have insured wider attention to an important paper than can be given it in its present voluminous form by any except special students of plant pigments.—C. R. B.

THE RECONSTRUCTION of the nucleus and the formation of the chromosomes in vegetative mitoses is the title of an important paper by GREGOIRE and WYGAERTS.[27] The material studied was the roots of *Trillium grandiflorum* and the homotypic division in the pollen mother-cells of *T. cernuum*. The conclusions in many cases differ decidedly from the commonly accepted views.

*Telophase in root tips.* After the chromosomes have reached the poles, one sees surrounding and bathing the mass of chromosomes the liquid which will constitute the nuclear sap. The liquid increases rapidly and causes the formation of the nuclear vacuole and nuclear membrane. On this point the writers are quite in accord with the recent view of LAWSON.[28] Each chromosome, through a gradual process of alveolarization, becomes resolved into a network, so that the entire nuclear network is a network of networks. In the resting nucleus within the membrane the chromatic network, lying in the nuclear sap, is (with the exception of the nucleolus) the only constituent. The nuclear membrane forms in immediate contact with the chromosomes, so that if any cytoplasm is included it is only a few

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[27] GREGOIRE, VICTOR, and WYGAERTS, A., La reconstruction du noyau et la formation des chromosomes dans les cinèses somatiques. I. Racines de *Trillium grandiflorum* et télophase homoeotypique dans le *Trillium cernuum*. La Cellule 21: 7–76. *pls. 1–2.* 1903.

[28] LAWSON, A. A., On the relationship of the nuclear membrane to the protoplast. BOT. GAZ. 35: 305–319. *pl. 15.* 1903.

threads of the central portion of the spindle which may become imprisoned. No karyoplasm is formed in the nucleus of Trillium. In passing through the telophase to the resting condition, no continuous spirem is formed.

*Prophase in root tips.* The nuclear network becomes resolved into alveolar or reticular pieces. A process of concentration and homogenization (*sit venia verbo*) continues until the chromosomes have the form of homogeneous rods. There is no continuous spirem in the prophase and the chromosomes never present the form of an achromatic ribbon carrying chromatic granules. The longitudinal division of the chromosomes begins by the formation of a series of chinks lying along its axis and not by the division of granules. In the nuclear cavity there are no granular or filamentous structures, but only the chromatin (and nucleolus) lying in the nuclear sap.

*Telophase of second division in pollen mother-cells.* No daughter thread is formed. The nucleus results from the confluence of one or more vesicles each of which contains one or more chromosomes. A chromatic vesicle in Trillium is a vacuole containing a chromosome bathed in nuclear sap. The nuclear membrane is formed by the condensation of the peripheral layer of cytoplasm bordering the nuclear vacuole.

The writers define the nucleus (excepting nucleoli) about as follows: In Trillium the nucleus is a vacuole limited by a cytoplasmic membrane, filled with a nuclear sap in which lies a chromatic network consisting of a homogeneous ground substance, without differentiation into an achromatic substratum and chromatic granules. The network, which arises from the juxtaposition of the networks of the individual chromosomes, apparently retains its composite character during the resting period, and so might be defined as an association of chromosomes which have become alveolar and reticular.—CHARLES J. CHAMBERLAIN.

STRASBURGER[29] in a very important paper on the reduction division expresses views which are quite opposed to his previous interpretations. The observations and discussion deal almost exclusively with the first division in the mother-cell, because there seems to be no ground for interpreting the second division as a reduction division. *Galtonia candicans*, the principal form studied, is particularly favorable, since it has only six chromosomes and is easy to stain. In the pollen mother-cell during the loose spirem stage of the first division the thread shows a longitudinal splitting, but the daughter threads do not separate. The thread becomes shorter, thicker, and simpler, and then divides into six chromosomes which are bivalent, as shown by the fact that each one splits transversely into two. Thus arise twelve chromosomes united in pairs. The pairs assume the various shapes so often observed. After the two parts of each pair have become separated and are nearing the poles of the spindle, a longitudinal fission can be seen. This is the longitudinal fission commenced but not completed in the loose spirem stage. The chromosomes become placed end to end, but are united only by linin threads,

[29] STRASBURGER, EDUARD, Ueber Reduktionsteilung. Sitzungsb. Königl. Preuss. Akad. Wiss. **18**: 587–614. *figs. 9.* 1904.

and are distinguishable during the short resting period.   In the second division the chromosomes split longitudinally along the line indicated in the loose spirem stage of the first division.   Consequently, it is the product of the first longitudinal division which becomes separated at the second division, and not the product of a second longitudinal splitting as believed by those who support the theory of a double longitudinal splitting.   The first mitosis is a reduction division, the second an equal division (*Aequationsteilung*).   Besides the figures of Galtonia, a series of diagrams makes the process easily understood.   An examination of Tradescantia gave approximately the same results, but in this form the processes are not so easily observed.   The much studied Lilium, though not a favorable form, will bear a similar interpretation.

The greatest difficulty in the investigation and the most important part of the discussion concerns the synapsis stage.   At this period the chromatin withdraws from the linin thread and collects around twelve centers (*Gamocentren*) corresponding to the twelve chromosomes.   The chromatin granules form loose groups, then unite to form bodies in which the separate granules can hardly be distinguished. These bodies elongate, become constricted in the middle, the granules of the two halves begin to separate, and with the aid of the linin form a continuous thread.   The entire thread then splits longitudinally.   That the twelve bivalent segments of this thread correspond to the twelve bodies counted during synapsis, and that the transverse division of each bivalent chromosome again separates halves of that body, cannot be doubted.   The view that there are differentiated chromosomes in the synapsis stage is consequently incorrect.   Rather, the chromatin content of the chromosome is in the form of small granules collected about a middle point, the number of these middle points corresponding to the reduced number of chromosomes and to the number of chromosome pairs.   One can actually see the granules form a body which becomes divided into halves. STRASBURGER conceives that the granules leave the linin thread that there may be a freer interchange among them than would be possible in the case of differentiated chromosomes.   He proposes the term *gamosome* for the individual chromatin granules, and *zygosome* for the body which they form.   From each zygosome comes two chromosomes, in the formation of which the linin takes part. The chromatic gamosomes are the bearers of hereditary qualities, the linin having only a secondary significance.   The diminution of chromatin during the resting period of the nucleus is not regarded as evidence that the chromatin is not the bearer of hereditary qualities.   In synapsis the individuality of the paternal and maternal chromatin is given up.   They unite to form a single zygosome, from which come two new chromosomes.   These two chromosomes do not contain exclusively paternal or maternal gamosomes.   This throws light on the differences in the offspring of a pair of parents and also upon the splitting of monohybrids.   In discussing the question whether each chromosome bears all the hereditary qualities of the organism, some evidence is found in favor of the view that the chromosomes are not of equal value.

A fuller presentation of these views and their relation to current conceptions would be welcome.—CHARLES J. CHAMBERLAIN.

# NEWS.

Mr. E. W. D. Holway has been appointed assistant professor of botany in the University of Minnesota.

Professor Girolamo Cocconi, a well known Italian mycologist, died at Bologna, October 6, at the age of 82.

Professor Gaston Bonnier of Paris has been elected a member of the Royal Microscopical Society of London.

August Franz LeJolis, the well-known French marine phycologist, died August 20 at Cherbourg, at the age of 81.

Mr. Clifton Durant Howe, instructor in the University of Chicago, has been appointed instructor in botany in the Biltmore Forestry School. He will enter upon his duties January 1, 1905.

A. H. Reginald Buller, of the University of Birmingham, has been appointed professor of botany in the University of Manitoba, Winnipeg, Canada, and assumed his new duties in October.

The address of Professsor F. O. Bower delivered at the International Congress of Arts and Science, St. Louis, September 1904, was published in *Science* of October 21. He discussed the relation of the axis to the leaf in vascular plants.

Commissioned by the Department of the Interior, the Swiss Scientific Society announces that it will award a stipend of 5,000 francs to enable some Swiss botanist to visit Buitenzorg. Applications are to be sent to Professor Dr. C. Schröter of Zürich.

The Botanical Magazine (Tokyo), in its September number, has begun to publish a résumé of its Japanese papers in some European language. This puts the contents of the journal within the reach of all botanists, and will avoid the compulsory neglect of interesting Japanese contributions.

The lectures given by Professor de Vries at the University of California are being edited by Dr. D. T. MacDougal and will appear in a volume to be entitled *Species and varieties; their origin by mutation,* to be published by the Open Court Publishing Co., of Chicago. The book is promised in January.

The United States Department of Agriculture has now two cooperating gardens established especially for the study of the date palm, one at Tempe, Arizona, and one at Mecca, California. In all probability a third garden may be established near Yuma. The thorough studies under way on the life history of this plant in connection with its introduction into practical culture promise to yield results of interest both to botanists and to horticulturists.

THE REPORT of the Imperial Botanic Garden of St. Petersburg for 1903 contains the following items of general interest: the collection of living plants comprised 34,887 species; during the year there were 40,296 visitors; the herbarium had an accession of 10,808 species (52,421 specimens); the library contained 14,986 works in 30,952 volumes. Attached to the garden are the biological laboratory, the seed-testing station, the central station for plant pathology, and the school of horticulture.

BOTANICAL SUBJECTS for the Walker Prizes have been announced as follows. For 1905, 1. "The life history of any parasitic fungus;" 2. "Contribution to our knowledge of the physiology of plants;" 3. "Study of hybrids in animals or plants;" 4. "Critical study of geographical distribution of species." For 1906, 1. "An experimental field study in ecology;" 2. "A contribution to a knowledge of the nature of competition in plants;" 3. "A physiological life history of a single species of plants;" 4. "Phylogeny of a group of fossil organisms." Address the secretary, GLOVER M. ALLEN, Boston Society of Natural History, Boston, Mass.

THE *Experiment Station Record* states that the order establishing the soil and fertilizer laboratory in the Bureau of Chemistry, U. S. Department of Agriculture, has been abrogated, and in lieu of this laboratory one to be known as the plant analysis laboratory has been established. The laboratory is charged with the examination of fertilizers and will collaborate in this work with the referees of the Association of Official Agricultural Chemists, and with the investigation of the constitution of plants. It is authorized to collaborate with the Bureau of Plant Industry in the chemical investigation of problems in which the two bureaus are mutually interested.—*Science.*

THE AMERICAN ASSOCIATION for the Advancement of Science will meet in Philadelphia December 27–January 2, and the many affiliated societies gather in the course of this convocation week. Thus, the eleventh annual meeting of the Botanical Society of America is called at this time under the presidency of FREDERICK V. COVILLE. CHARLES R. BARNES, the retiring president, will give an address on *The theory of respiration.* By invitation of the Council special papers will be presented by Professor BALFOUR of Edinburgh and Professor VÖCHTING of Tübingen. On Dec. 28–30, the eighth annual meeting of the Society for Plant Morphology and Physiology will be held. Doubtless the Mycological Society will meet in Philadelphia also in the same week, though announcements have not yet reached us.

There is every indication that these meetings of botanists will be of unusual interest and importance. Among other matters to be considered will be the plan for a union of the botanical societies. Preliminary suggestions for such a union have been sent by the committees of conference to all members for their consideration, and the replies received will be used as a basis for the formulation of a definite plan which will be sent to all members before the meeting. This plan will then form the basis for the discussion at the meetings and for the decision for or against a union.

# BOTANICAL GAZETTE

## *DECEMBER, 1904*

### THE VARIATION OF SOME CALIFORNIA PLANTS.

Edwin Bingham Copeland.

(WITH NINE FIGURES)

### I.

ONE of the first features of the flora of the mountainous and rather dry parts of California to impress one familiar with that of the eastern states and the Mississippi valley is the exceeding variability of a great many of the plants. While every botanist going into this field must have been struck by this fact, and some have remarked upon it, as JEPSON well does in the introduction to his *Botany of Middle Western California*, it has never been the subject of any particular study.

The good material for such work is practically unlimited; but my time has not been so, and it has seemed to me that the study of a few plants ought to show what is most characteristic of variation in this region. I have found that the study of these few has given me a plausible explanation of the great local variability, and at the same time has strengthened views already held as to the commonness of variation at other times in the history of plants beside their conception, and as to the generic homogeneity of continuous and discontinuous variation. Out of the material I have worked over, it will suffice for all purposes if I describe the variation of a few woody plants of wide occurrence, and of a few apparently monstrous ferns and the lesser variations connecting them with normal forms. The woody plants selected are several oaks growing near Palo Alto or Chico, and *Rhamnus californica, Arctostaphylos tomentosa, Ceano-*

*thus sorediatus*, and *Baccharis pilularis*, shrubs of the Palo Alto
neighborhood, of frequent occurrence and reasonably independent
as to altitude, soil, and exposure.  As a further limitation, this account
is confined with a single exception to the leaves of these plants; varia-
tion in other features—for instance in the scales of the cup of Quercus
—is not less conspicuous.

### Quercus chrysolepis Liebmann.

The leaves of oaks are exceedingly variable everywhere, but the
differences between the leaves of this species on the same tree, or on
neighboring trees, are conspicuous even in such a genus.  *Figs. 1–3*
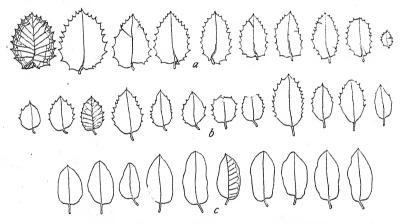


Fig. 1.—*Quercus chrysolepis: a*, alternate leaves on a branch; *b*, all the leaves on
a twig; *c*, all the leaves on a twig.  In all series from left to right is towards the apex.

are from neighboring trees, growing in the mountains back of Stan-
ford University.  Each tree had a well-defined leaf character, as
these outlines, each representing leaves of one season's growth on one
axis, indicate.  The venation of the leaves on each tree was as charac-
teristic as the outline.  As a rule, older trees have more entire leaves,
but this is not at all constant; all my specimens are from acorn-bearing
trees.  All the leaves figured grew on well-illuminated parts of the
trees.  In the three trees furnishing these leaves the variation in leaf-
character was an attribute of the entire tree, and must therefore have
occurred at a time in the tree's history when it or the stage in its
ancestry where the variation occurred was a single cell, or (possibly)

at most a small and homogeneous group subject to a common impulse. We are in the habit of thinking of variations as concerning entire organisms.

More frequently, however, such leaf forms as these are not so strictly characteristic of whole trees; but single twigs show uniformly aberrant types of leaves; or most often single or few leaves of divergent forms are found scattered over the tree. *Fig. 2, a* represents the leaves of a single twig on which the leaf character changed profoundly during the season. This might have been ascribed to a change in the available water during the season, but that not all the twigs of the tree
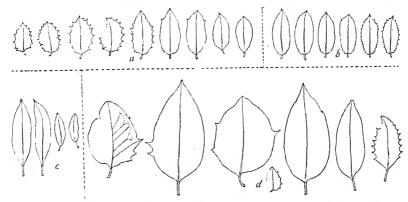


Fig. 2.—*Quercus chrysolepis: a*, all the leaves of a twig; *b*, younger leaves of a twig; *c*, consecutive leaves; *d*, some leaves on one season's growth of a twig.

behaved in this way. *Fig. 2, b* shows the opposite change in the same season's growth, on another specimen from Chico; and *fig. 2, c,* representing four successive leaves on one twig of the same tree, shows how abruptly the size, as a character of the twig, may change. *Fig. 2, d* shows outlines of a number of leaves on one season's growth of a twig; in this case variation seems to have occurred not in the apical meristem giving rise to both axis and leaf, but in the primordia of the individual leaves.

### QUERCUS DUMOSA Nuttall.

All of the figured leaves of *Q. dumosa* were collected in a single small patch of chaparral, on exposed parts of mature shrubs; their differences are therefore independent of the environment. *Fig. 3, a–b* are all the leaves of the last season's growth on two twigs of the

same shrub, showing variation in the shape of the leaf as a character of the twig. *Fig. 3, c* shows single leaves from other parts of the same shrub, illustrating variation in single leaves. *Figs. 3, d, e* represent the characters of the shrubs as the varying entities; the shrub from which *fig. 3, d* was made bore conspicuously narrow leaves throughout, while *fig. 3, e* is from an example of the well-known bullate variety. This strain is so pronounced that it has been regarded as worthy of a distinct name; but it intergrades with the more typical form, and flat more or less spiny leaves are sometimes found on the same shrubs with the most bullate ones.
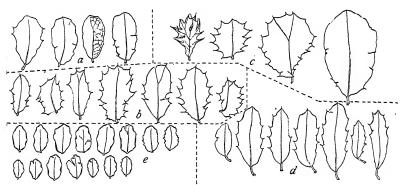


FIG. 3.—*Quercus dumosa: a*, all the leaves of a twig; *b*, all the leaves of a twig from same plant; *c*, single leaves from same plant; *d*, leaves of a twig of a bush with prevailing narrow leaves; *e*, leaves from the bullate variety.

## QUERCUS WISLIZENI A. DC.

In the Santa Cruz peninsula *Q. Wislizeni* is a characteristic tree of the hilltops. In its typical situations it is less constantly and conspicuously variable in shape than the two species just considered. In protected spots it varies more noticeably, but as the influence of the environment may be directly expressed in these cases, they are left out of account. About Chico this is the common live oak of the valley, and is also common in the hills, and is as variable as *Q. chrysolepis* or *Q. dumosa* in that region. As in these, variation is by the tree, the branch or twig, or the single leaf. The difference between neighboring twigs on the same tree is illustrated by *fig. 4.*

## QUERCUS AGRIFOLIA AND OTHER OAKS.

*Q. agrifolia* Née is the commonest live oak of the valley and lower hills about Palo Alto. It varies in the shape, size, thickness, and pubescence of the leaves, and like all the preceding may be entire or very much toothed. Variation is by the tree or any part of it, but is by no means so extreme and chronic as in the oaks I have illustrated; in other words it breeds truer to a type. The other live oak of this region, *Q. multiflora*, is quite restricted as to its habitat; its variation is inconsiderable. Among the deciduous oaks, *Q. Kelloggii* Newberry, which is common in the foothills and mountains, is most variable in its foliage (and fruit); decidedly more so than *Q. lobata* Née, the great
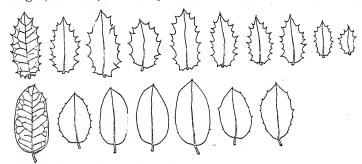


FIG. 4.—*Quercus Wislizeni:* all the leaves on two twigs of the same tree.

white oak of the valleys. In the mountainous north end of the state, *Q. Kelloggii* is still very variable, as is the *Q. Garryana* Dougl., found with it. On the slopes of Mt. Eddy, *Q. vacciniifolia* Kellogg, ranging from the foot of the mountain up in an extreme case to well above "timber line," has as variable leaves as *Q. chrysolepis*. The leaves of the small oak of the moist wooded valleys of this region, known as *Q. multiflora*, are very uniform in all respects; but quite unlike those of the *Q. multiflora* of the south.

In the cases of all these oaks the fact cannot be too strongly emphasized that I have been discussing only real variation, as independent of any influence of the environment as experiment could have made it. The influence of differences of environment, wherever they exist, is very evident, and has been broadly handled by BRENNER.[1] He points out the great differences the environment causes

[1] BRENNER, W., Klima und Blatt bei der Gattung Quercus. Flora **90**:114–160. 1902; also Zur Entwickelungsgeschichte der Gattung Quercus, *idem* 466–470.

between the leaves of different trees, and even the leaves unequally exposed on the same tree; which naturally makes him skeptical of the value of determinations of extinct oaks by the remains of their leaves.   The variations independent of the direct action of the environment, which I have just depicted, must strengthen the skepticism.

Before leaving the subject of Quercus I wish to discuss briefly BRENNER'S conclusions.   He regards the less stability of the lobed forms of leaf as compared with the entire as evidence of the greater antiquity of the latter; such a difference in their *variability*—which should be a better test of newness than stability under varying environment—does not exist in this region.   Still, considering oaks the world over, BRENNER may well be correct on this point.   In his concluding paragraph, however, he exposes a classical weakness which needs pointing out as often as it occurs.   It reads:

Was als wichtigstes Ergebnis aus derartigen Untersuchungen hervorgehen dürfte, ist die so oft noch bezweifelte Thatsache, dass die durch äussere Medien hervorgerufenen Veränderungen an den Pflanzen thatsächlich erblich werden und im Lauf der Entwickelung zu eigentlichen Artmerkmalen sich entwickeln können.   Durch den Nachweis, dass bei den Eichenblättern die Veränderungen beim Versuch und bei natürlichen Standortsunterschieden den mit dem Klima wechselnden Speziesverschiedenheiten entsprechen, hoffe ich einen Theil zur Kräftigung dieser Anschauung beigetragen zu haben.

If one accepts the inheritance of acquired characters *a priori* as "Thatsache," he may construe BRENNER'S observations as an illustration of it.   But the direct reaction to the environment is fairly to be regarded as the result of natural selection, developed and preserved by virtue of its appropriateness; and since it is appropriate, it is obvious that by natural selection alone the plants varying in this direction spontaneously would be at an advantage, and in the long run would be parents of all the offspring.   Since the identity of the forms assumed as a direct response to the environment with the forms characteristic of lands with the corresponding climate is fully explicable by natural selection alone, it is certainly no valid argument in favor of the inheritance of direct reactions to the environment.

My oak leaves will be discussed with those of the other woody plants.

## RHAMNUS CALIFORNICA Esch.

In the foothills and mountains back of Palo Alto, *R. californica* and its var. *tomentella* Brewer and Watson are scattered promiscuously and merge by insensible gradations. The distinctions are supposed to be that the variety has tomentose reddish twigs, leaves yellow or white tomentose beneath, and peduncles longer than the petioles. My material was not collected at a season to illustrate the last feature. As to the others, individual shrubs possess or want them, so that a collector might easily gather material of the type or the variety; but in the field there is no constant relation between the color of the stem and the tomentum on the leaf, and neither green nor red twigs are likely to be glabrous. The leaves also vary notably in outline, apex, thickness, and margin, and in the rolling back of the sides. The most remarkable variability is in thickness and texture, margin, and pubescence. I have measured the length, breadth, and length of petiole of all the leaves on one twig (one year's growth) of twenty-eight bushes. In the following table the results, averages for each bush, are arranged according to the shape of the leaves, the ratio of breadth to length, because this ratio is a feature that can be exactly expressed, and one that could not possibly have been considered in the collecting. This ratio is of average width to average length, and is usually larger than the average of the ratios for the individual plants.

Further explanation of the table is as follows: under "margin" *s* is serrate, *ss* subserrate, *e* entire; under "lower surface" *g* is green and apparently glabrous, *wg* pale green and moderately pubescent, *w* white (sometimes yellow) and very pubescent; under "reflex" is given the per cent. of leaf folded back when pressed fresh; under "stem" *g* is green, *rg* reddish-green, *r* reddish, *rr* red; thickness is stated in units of a spherometer.

The length of the petiole is not significant. The width of the leaves is omitted from the table because expressed in the shape; it is less variable than the length, wherefore the average length of the relatively narrow leaves (55.7$^{cm}$) is greater than that of the rounder ones (47.3$^{cm}$). I did not attempt greater accuracy of description of the margin than calling it entire, subserrate, or serrate. This placed a majority of the leaves in the middle class, which includes leaves with a few prominent teeth irregularly scattered or only near the apex, or few or more numerous closely appressed teeth, or rarely

TABLE I.

| Shape | Length in mm | Margin | Lower surface | Reflex | Stem Color | Leaf thickness |
|---|---|---|---|---|---|---|
| 1.8 | 25.4 | ss | w | 9 | r | 139 |
| 1.9 | 62.9 | ss | g | o | r | 102 |
|  | 27.8 | e | wg | 2 | rg | 106 |
| 2.0 |  |  |  |  |  |  |
| 2.1 | 73.1 | s | g | o | g | 48 |
|  | 51.1 | ss | wg | 2 | rg | 93 |
|  | 34.0 | e | wg | 29 | rg | 122 |
|  | 30.3 | ss | w | 34 | r | 164 |
| 2.2 | 48.5 | e | w | 36 | g | 182 |
| 2.3 | 70.8 | s | g | o | rr | 62 |
|  | 62.8 | ss | wg | 3 | rg | 89 |
|  | 50.1 | ss | g | 13 | rr | 148 |
| 2.4 | 47.0 | ss | g | 2 | rr | 102 |
|  | 50.0 | ss | w | 1 | r | 127 |
|  | 29.0 | ss | wg | 17 | r | 118 |
| 2.5 | 46.6 | s | g | 3 | rr | 100 |
|  | 43.5 | e | g | 17 | r | 118 |
| 2.6 | 55.4 | ss | wg | o | rr | 178 |
|  | 50.0 | e | wg | 40 | rr | 126 |
|  | 38.7 | e | wg | 33 | r | 149 |
| 2.7 | 114.6* | s | g | o | g | 58 |
|  | 35.7 | e | w | 25 | rr | 196 |
| 2.8 | 61.5 | ss | wg | 6 | r | 181 |
| 2.9 | 61.7 | ss | wg | o | r | 92 |
|  | 46.7 | ss | wg | 1 | rr | 132 |
| 3.0 |  |  |  |  |  |  |
| 3.1 | 58.0 | ss | wg | 3 | r | 134 |
| 3.2 |  |  |  |  |  |  |
| 3.3 | 43.7* | e | w | 20 | r | 174 |
| 3.4 | 66.5 | ss | wg | 24 | r | 154 |

very numerous very minute teeth, so small as to give the appearance of none at all. Various parts of subserrate leaves may be entire. I could have counted teeth and reached a quantitative expression of the serrateness of some leaves, but the entire parts of leaves and the great difference in the teeth made such data rather meaningless. As the lower surface is described, the majority again of course occupies the broad middle ground, but there is no tendency toward any particular part of it.

These specimens were all collected in the vicinity of Woodside (a post-office a few miles from Palo Alto), which avoided the chance of extending the apparent range of variation by introducing geographical varieties. Selection of extremes in any direction was also avoided, by such devices as choosing a bush at too long range to more than

recognize it.[2]   Only the two starred in the table were collected after
my attention was attracted to them by their many differences; they
grew with interlacing branches in open ground by a roadside.   No
well-shaded bushes were chosen, nor shaded branches on the bush.
While the immediate environment of the leaves was thus eliminated
as a factor in making them different, the condition of the roots was
left uncontrolled.   I have no doubt that docking its roots would
cause one of these shrubs to produce thicker, rounder, and more
entire leaves, and I believe that these would tend to be pubescent
beneath and rolled inward.   But no visible differences in the ground
were associated with the different variations.   That the correlated
variations are not common functions of any outside agent is evidenced
too by their measure of independence—flat pubescent, entire green
leaves, etc.   The data in the table do not approach the range of
variation of the individual leaves nor indicate the frequency with
which the usually correlated variations are otherwise combined.
The frequent correlation of thickness of leaf with pubescence, rolling
backward, and evenness of margin might be due to such a com-
bination of characters in heredity as many recent writers on inheri-
tance assume; but I would rather ascribe it to mechanical factors
which operate as the plant grows.

The range of the variability of this Rhamnus is not more remark-
able than the absence of any well-defined type from which variation
can be regarded as taking place; or, to express it in the usual way, in
terms of curves, the curve representing any one of the varying char-
acters under discussion would be conspicuously broad and low,
without a well marked maximum and steep slopes.   That this is
true for the shape of the leaf the tabulated arrangement shows.   If
a curve were plotted with abscissae of 0.2, beginning with 1.7, the
ordinates would be 1, 2, 5, 6, 5, 3, 2, 1, 2.   If the length were plotted
as a curve with abscissae of $1^{cm}$ (40 per cent. of the shortest leaf),
the ordinates would be 3, 4, 6, 6, 5, 2, —1.   If a curve were made to
represent the thickness, with abscissae of 20 units of the spherometer
(over 40 per cent. of the thinnest leaf), the ordinates would be 2,

[2] I have one branch of whose leaves the ratio of average length to average width
is 4.25 : 1.00, but as I noticed its slender leaves before collecting it is not included in
the table.

1, 3, 6, 6, 3, 3, 3; or if the abscissae represent 40 units, beginning with 40, the ordinates become 3, 9, 9, 6. The shape curves of variation of this plant must be clear from these three illustrations. Of course, the curve could be made steeper and narrower by increasing the value of the abscissal units; but by this process, if carried to an extreme, any curve can be reduced to a vertical line; and 40 per cent. of the shortest or thinnest leaf ought to be a large enough unit. The curves for the entireness of the margin and the pubescence of the lower surface would be of the same shape as these if there were scales by which they could be measured. These numbers are too few to make symmetrical curves, but as an objection to the validity of the conclusions this is largely removed by the fact that each number is an average of a considerable number of measurements.

## ARCTOSTAPHYLOS TOMENTOSA Lindl.

This is the common manzanita of this region. Some authors have detected more than one species in what I include in it, but I am sure nobody would do so on my material. It was all collected in a limited region near the top of the mountain south of Woodside, using the same care to preclude the influence of local differences of environment as in collecting Rhamnus. Variable as it is, the manzanita has proved a much less favorable subject for this work than the Rhamnus, for several reasons. The most variable feature is the pubescence of both stems and leaves, and I have not found it feasible to measure this, because the chaff varies in size as well as in abundance, and is irregularly deciduous. Another difficulty is that the leaves formed at the ends of the seasons are smaller, narrower, and more entire than those typical of the plants; this made it necessary to discard some of the leaves, and to decide more or less arbitrarily where the typical leaves ceased on each axis. As this left too few leaves on each axis to furnish a safe average, I used all the fit leaves on the twigs of a small branch of each shrub. Tables II and III give the averages from thirteen plants, and the details of the individual leaves of one plant, to show their individual variability. The data under "margin" show the average number of teeth on each side of the leaf, and the average per cent. of the distance from base to apex at which the most apical tooth is found. Under base and apex their angles are given.

## TABLE II.

| Shape | Length | Margin | | Base | Apex |
|---|---|---|---|---|---|
| | | Teeth | Serrate % | | |
| 130 | 32.6mm | 0.0 | 0.0 | 187.0 | 146.0 |
| 153 | 39.8 | 0.0 | 0.0 | 190.0 | 121.0 |
| 153 | 39.9 | 1.5 | 24.0 | 184.5 | 97.0 |
| 154 | 37.0 | 0.5 | 14.0 | 168.0 | 112.0 |
| 155 | 46.2 | 0.0 | 0.0 | 172.0 | 133.0 |
| 162 | 38.2 | 0.55 | 8.5 | 178.5 | 97.5 |
| 169 | 29.5 | 0.25 | 3.75 | 137.0 | 126.0 |
| 175 | 39.3 | 0.2 | 4.0 | 188.5 | 96.5 |
| 180 | 37.1 | 8.8 | 63.0 | 161.0 | 96.0 |
| 184 | 41.5 | 2.7 | 37.0 | 170.0 | 106.0 |
| 190 | 31.8 | 0.0 | 0.0 | 217.0 | 108.0 |
| 198 | 32.0 | 0.1 | 2.0 | 181.0 | 95.5 |
| 202 | 42.4 | 0.0 | 0.0 | 169.0 | 123.0 |

## TABLE III.

| Length | Width | Margin | | Base | Apex |
|---|---|---|---|---|---|
| | | Teeth | Serrate % | | |
| 49mm | 27mm | 4.0 | 50 | 175 | 90 |
| 46 | 25 | 2.0 | 25 | 165 | 120 |
| 43 | 28 | 4.0 | 80 | 195 | 120 |
| 46 | 24 | 5.0 | 30 | 165 | 90 |
| 47 | 23 | 1.0 | 15 | 165 | 95 |
| 47 | 28 | 3.0 | 30 | 195 | 120 |
| 30 | 19 | 13.0 | 85 | 150 | 90 |
| 45 | 23 | 0.5 | 10 | 165 | 130 |
| 39 | 21 | 1.0 | 30 | 180 | 115 |
| 41 | 22 | 3.0 | 50 | 150 | 90 |
| 48 | 25 | 2.0 | 55 | 150 | 90 |
| 40 | 21 | 2.0 | 30 | 170 | 75 |
| 31 | 18 | 0.0 | 0 | 155 | 120 |
| 42 | 23 | 2.0 | 20 | 150 | 105 |
| 40 | 21 | 1.0 | 20 | 180 | 100 |
| 43 | 22 | 4.0 | 45 | 160 | 100 |
| 42 | 24 | 3.0 | 60 | 165 | 120 |
| 35 | 17 | 0.5 | 10 | 135 | 135 |
| 34 | 19 | 0.0 | 0 | 165 | 120 |
| 46 | 23 | 1.0 | 25 | 165 | 120 |
| 41 | 20 | 2.0 | 25 | 150 | 95 |
| 38 | 22 | 5.0 | 60 | 180 | 100 |

## Baccharis pilularis DC.

This is the most abundant shrub in the country about Palo Alto, growing practically everywhere. If *B. consanguinea* DC. is a distinct species, it does not grow here. The leaves (of *B. pilularis*) vary greatly from plant to plant, and also on the same plant. The size of the leaf varies on every plant with the order of the branch it is borne on; which made it so difficult to select a considerable number of leaves from different plants that as a whole should be fairly comparable that I did not try to make a table, but have preferred to reproduce the largest leaves from a few plants in a figure. *Fig. 5* shows the largest leaf of each of seven plants. Of two of these
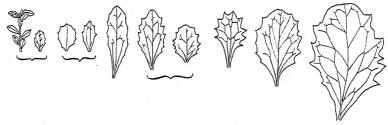


Fig. 5.—*Baccharis pilularis:* largest leaves of seven bushes.

plants two leaves each are drawn, to show the difference in shape. Of these seven, the most exceptionally large leaf, on its own plant was the smallest of the lot, the most of the leaves on that plant being like those on the twig figured.

## Ceanothus sorediatus H. & A.

The two commonest and most ubiquitous species of this genus about Palo Alto are *C. sorediatus* H. & A. and *C. cuneatus* Nutt. The latter is the common one of the valley and is rather the more variable, but I have not material to illustrate its variation in any one place. The plants of *C. sorediatus* from which *fig. 6, a* was made were collected in a small patch more than half-way up the mountain south of Woodside. Each leaf drawn was the largest on its branch. Beside the difference in size and shape, there is an uninterrupted variation, which my figure only suggests, from the dentate form, which I suppose gives the species its name, to one with quite entire leaves; and variation on the individual plants as well as between them.

Why are very variable plants common in this region? Because of the great local range in environments. There is a very strong probability that the offspring of a plant in the level east will grow under substantially the same conditions under which its parent grew, and that this will be true generation after generation. Under such conditions, variations fitting the plant in the slightest degree to its environment will in time be selected and will become specific characters. That even the most minor differences which serve as specific or even as varietal characters have the selection value this assumes I have not the least doubt; for they surely are not there to distinguish the species, nor for the sake of uniformity. It is heredity, acting within bounds established by the rigor of natural selection, that limits variation everywhere. In the mountains of the eastern states conditions are in most places hardly less uniform than in the great valleys; the seed may be carried as far as possible, but the seedlings will grow under conditions like those of their parents.

When one of these Californian shrubs or trees scatters its seed, there is a strong probability that the plants which grow from some of them will find themselves in surroundings decidedly different from those of their parents. Soils differ more in new and mountainous than in old and level countries. A difference of some 2000 feet in altitude, with a corresponding difference in temperature, is possible among the offspring of any one of these plants; and these are but minor differences in environment, the moisture and wind factors being the important ones. Some of the descendants of one of these plants may start to grow on high ridges swept by ocean gales; others on lower, only less windy, very dry and hot ridges and hilltops; others in the chaparral, dry and hot, but protected from wind; others in the fog-soaked passes, sheltered from most winds; and still others in the cañons, or rather gulches, deep and shady enough to keep the air fairly moist and still at all times.

If a plant grew in this region whose lack of variation enabled it to produce offspring uniformly well adapted to any one environment a large part of its seeds would be likely to fall where the seedlings must start to grow under conditions for which they were but ill suited; while a variable plant growing here has some chance that its offspring, wherever they find themselves, will be more or less at

home. Since they all produce seed far in excess of what can grow, this means that in time the descendants of a variable plant will be found in considerable numbers under very different conditions; and that in this way it will be able to have many more descendants than the non-varying plant, the space available to whose offspring is limited. More descendants bear more seed, likewise variable, and with that they will thrive wherever they fall. And so the variable plant has some advantage in competition with the specialized one even where the latter is at home.

Where the environment is uniform over great areas, then natural selection breeds very close to a type, and considerable variation is a disadvantage; but where there are great and constant local differences in environment the premium is taken off of specialization, and natural selection favors a relatively high degree of variability. In such a place we find not merely that plants vary with the environment, but that in any single spot the individuals vary conspicuously as well.

If this is the real explanation of the variability of these plants, it is to be anticipated that plants of restricted range and characteristic habitat in this same locality will be more specifically adapted to their particular habitats, and when growing side by side with the ubiquists will be less variable. I have already pointed out that this is true among the oaks. The only other Rhamnus of this neighborhood, *R. crocea*, is not abundant enough even in spots to prove anything. In each of the other genera I have used, Arctostaphylos, Baccharis, and Ceanothus, we have other species of relatively local occurrence and relatively limited variability.

*Baccharis viminea* DC. is a plant of local occurrence on the flank of the mountains. Its leaves are sometimes entire, at other times sparsely serrate toward the apex; otherwise it is very constant. *Arctostaphylos Andersonii* Gray grows only near the mountain tops in the fog belt. The following measurements are of five plants selected in the field to show the extremes of variation; twenty-seven plants selected as were those of *A. tomentosa* would probably have varied less widely than these five do. No entire leaves were found.

```
Shape:      161,   169, 200, 203, 207
Length:      35.5, 44,  54,  46,  41.9
Serration %: 18,   76,  29,  36,  29
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*Ceanothus papillosus* T. & G. is strictly confined to ridges in the fog belt, and is correspondingly constant. *C. thyrsiflorus* Esch. comes farther down the mountains, but not to their foot, and avoids exposed situations. The subjects of *fig. 6, b* were collected in the same place with those of *fig. 6, a*, at the same time and in the same way, before I realized that there was a difference in the variability of the two species, or suspected the reason for it. The contrast of the two is very striking.

## II.

Some time ago I published a very brief note[3] on some freak ferns found in West Virginia, and suggested at the same time the interest of such freaks when the relation of minor and more conspicuous
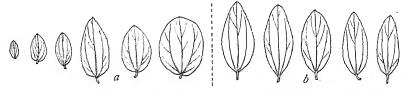


FIG. 6.—*a, Ceanothus sorediatus:* largest leaves of six shrubs.   *b, C. thyrsiflorus:* largest leaves of five shrubs.

variations was being vigorously disputed. Since that time the mutation theory has lost none of its interest and probably none of its prestige. Meantime I have collected many more freak ferns, and some very full series illustrating less unusual variations; of these as many are presented here as seem necessary to justify the view that ordinary variations are indefinite in range and that extremes of series of such variations would be regarded as sports or mutations if found or collected alone. A detailed argument on this point with each fern shown would be superfluous. As in the former paper, I rely on figures rather than words to describe some of these ferns.

The variation in the extent to which some ferns are serrate, pinnatifid, or pinnate is very familiar. *Aspidium munitum* Kaulf. is usually only moderately serrate, like *fig. 7, b.* It varies in one direction to a form with teeth so closely appressed that at a distance it appears entire, and in the other to a form with compound teeth,

3 BOT. GAZ. **34**:142–144. 1902.

incised more than a third of the way to the midrib. *A. aculeatum*
Swtz., in several varieties endowed with names, but freely merging,
varies from a form but little deeper cleft than the most incised form
of *A. munitum* to one in which these teeth become pinnae which in
turn are cleft to the midrib into toothed divisions; that is, it varies
from pinnate to tripinnate, the most
divided part of fertile fronds being
considered in every case. This
variation could be duplicated in
many ferns. It is doubtless continu-
ous; but many of our fern species
are founded on differences so small
that a series of them would not
bridge the gap between the extremes
of this variation.



FIG. 7.—*Aspidium munitum:* teeth
from six fronds, all drawn to same scale.

*Fig. 8* is a fragment of a very
abnormal frond of *A. argutum*
Kaulf. Such freaks are not
exceedingly rare. Some pinnae are usually normally developed; and
there are all stages between these and mere lumps marking the place
where pinnae should
be. These freaks are
almost always sterile,
as other very abnor-
mal ferns are likely
to be. Reproduction
is the consummation
of normal develop-
ment, and any devia-
tion from the usual
course is likely not to
lead to this end. Of
course, this is not true
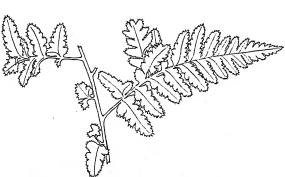


FIG. 8.—*Aspidium argutum:* part of abnormal
frond.

of ferns alone. I have found sterile freaks of a number of flowering
plants among fertile normal forms. Reproduction demands a
decidedly more perfect concatenation of favorable external and
internal conditions than does growth.

There are several different lines of interesting variation of *Poly-podium californicum* Kaulf.  One of these is the elongation of the pinnae, some or all of them, on a frond.  Fronds noticeably more acute than the normal are not rare, but of course the more extreme variations are proportionately seldom found.  I have some twice as long as the normal; but none so con-spicuous in this respect as the *P. vulgare* from West Virginia, in my other note on this subject.  Another line is the increase in the size of the teeth and the deepening of the incisions between them until the pinna is pinnatifid, even to the midrib on the lower side.  In this case the number of times the veins are forked is greatly increased, which disturbs one charac-ter often deemed specific in Polypo-dium; and the veins all remain free, which would be more notable if the separation of Goniophlebium as a dis-tinct genus were natural.  In merely serrate plants the union of the veins to form areolae of the Goniophlebium type may or may not occur, the anasto-mosis or its failure being utterly with-out rule, even on single fronds or single pinnae.

The anastomosis is likewise irregu-lar in the fern known as *P. Scouleri* Hook. & Grev., which is so unstable in other respects that it would as well be considered a form of *P. californi-cum*.  Down close to the beach, where the typical form of *P. Scouleri* is found,
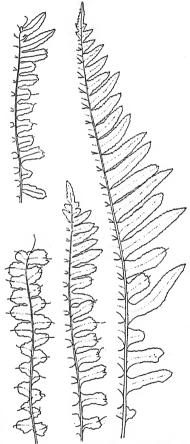


FIG. 9.—*Polypodium californi-cum:* a series of abnormal fronds.

it is variable, there being from three to twelve pairs of pinnae, which are "typically" twisted and thrown forward until they all fold in pressing, but are sometimes perfectly plane.  Where more protected

they are thinner, with more acute pinnae. To what extent *P. Scouleri* represents the direct action of the environment, and to what extent it has developed into a really independent species can only be determined finally by experiment, but certainly it is very variable, and is also profoundly modified by the environment. Its variability is evidence on the point demonstrated by the oaks and shrubs.

A most remarkable monstrosity, many individuals of which have lost all characteristics of *P. californicum* and are indistinguishable from a freak of *P. vulgare* reported from Germany, was first found near Chico, where it had complete possession of a small patch of ground (*fig. 9*). Its essential feature is that the distal part of the midrib of the lateral pinnae and segments, and the whole axis of the terminal one, develop no wing, but spring free from the spore-bearing surface of the blade. In correlation with this, the growth of the segments is arrested, making their apices round and dentate, and the frond as a whole truncate-oblanceolate. The free part of the midrib may be prolonged to at least the natural length of the segment; or may be shorter, even to the extent of not springing free at all; in which case the development of the blade may be anywhere from very stunted to normal. All the pinnae may be affected; or some of them toward the apex may not; or only a few or a single one may be modified, making a complete series from normal fronds to the most monstrous. Since collecting it near Chico, I have twice found a few ferns like these back of Palo Alto, but in these only a part of the segments were ever malformed.

### III.

I wish now to use this material, both the shrubs and the ferns, as the basis for a discussion of the "mutation theory" in bionomics. It is already clear enough that I do not believe there is any foundation at all for the view that mutations as essentially distinct from ordinary variations exist. That they do not I endeavor to show. But the mutation theory under one or another caption has for years been a refuge for those who on any ground regarded natural selection as inadequate to the demands upon it, and has recently been so powerfully supported by DE VRIES and others (BATESON, WETTSTEIN, etc.), and has been so enthusiastically received that it has become

a proper subject for discussion by those who recognize no ground for it.

The mutation theory does not, as some of its supporters seem to believe, do away with the doctrine of natural selection.   This doctrine is that among more living things than can live and bear progeny those best adapted to the existing environment will survive.   It assumes, what is the fact, that the existing organisms differ.   The mutation theory would explain the origin of the differences, saying that from their first appearance they are too wide and fundamental to fall in the category of "individual variations."   The more prevalent idea since DARWIN has been that these minor, incessantly appearing differences were the raw material for nature to select among, and that by the constant survival of the individuals with the slightest advantages new races, varieties, and species might arise; but every partisan of natural selection recognizes variation as prerequisite to any evolution.   The apparent issue is: "are the differences whose perpetuation gives rise to new species the ordinary individual variations, or the less usual but more considerable mutations?"   But a question which should obviously be settled first is: "are individual variations and mutations distinct?"

Since I do not believe that the differences between the offspring of common parents differ fundamentally among themselves, it is but natural that I should be unable to frame a definition of a mutation which would really distinguish it from the general run of variations. For the most authoritative definition I have consulted DE VRIES's *Mutationstheorie.*   To my surprise, I have read the book, and then very carefully re-read the general part, without finding anywhere anything that has the force or form of a definition.

In the introduction, where "es sich darum handelt, den Unterschied der beiden Grundformen der Variabilität so klar wie möglich darzuthun," he says: "Die Mutationen sind Vorgänge, über deren Natur wir noch sehr wenig wissen.   Die bekanntesten Beispielen solcher Mutationen sind die sogenannten spontanen Abänderungen ('single variations'), durch welche scharf unterschiedene neue Varietäten entstehen.   Man nennt sie auch wohl Sprungvariationen" (p. 4). Again he says (p. 22): "Die letzteren [single variations] sind zufällige, spontane Abänderungen, unseren Mutationen *entsprechend*"

(italics mine).  And (p. 23): "Die *single variations* sind zufällige, nur von Zeit zu Zeit auftretende, sprungweise die Formen verändernde Erscheinungen."  He says (p. 5): "Die Gesetze der Mutabilität sind ganz andere als jene der Variabilität;" but this clue to the distinction fades when we read (p. 23) that "Die 'single variations' sind zufällige Erscheinungen, von deren Gesetzen man bis jetzt keine Erfahrung hat."

Calling single variations and saltatory variations and discontinuous variations synonymous with mutations does not tell what any of them are.  The one criterion by which DE VRIES tries consistently to distinguish mutations is their giving rise to specific characteristics.  This certainly does not admit of practical application, because we do not know how to identify a specific characteristic.  It is a very tenable position at present that the species is a group of organisms with limits set by our convenience, and that many "valid" species—to put it moderately—are characterized by distinctions which are matters of degree.  The specific characteristic can hardly be more clear-cut than the species it characterizes.  If specific characteristics are in nature unstable and not exactly definable, this one means of identifying mutations is imaginary, in addition to being inapplicable.  DE VRIES holds that species, not necessarily with the usually recognized limits, are definable and never have merged, and that their individual characteristics are likewise definable and stable; but when he identifies these in turn by their origin by mutation, he brings his argument into a circle.

The practical characteristic of mutations on which DE VRIES lays most emphasis is their inheritance: "Solche sind fast stets entweder völlig oder doch in hohem Grade erblich" (p. 16).  But, as he of course recognizes, the continuous individual variations are also hereditary.  We see that on every hand.  The most familiar examples are furnished by human beings.  DE VRIES says explicitly that the differences between them have not arisen by mutation as he uses the term.  Yet what characteristic of any species is more certain to be inherited than the straight hair or the black hair of a pure Chinese, or the complexion of an Ethiopian or an American Indian?  Among the much less constant features of our own race we know how likely the color of the eyes and hair, and other physical peculiari-

ties, and even mental eccentricities, are to be inherited.   On the other hand, mutations are not always inherited, as De Vries's observations on Oenothera show; and if they were, there could be no mutations. Variations certainly differ in the reliability with which they are inherited; but mutations, if there were such, would not be distinguishable from other variations in this respect, unless sometimes in degree.

Many authors have sought to distinguish single variations or discontinuous variations from the continuous individual variations by the extent of the deviation from the parental type.   De Vries does not lay himself liable on this point, saying explicitly that they are not distinguishable in this way (p. 41): "Die Betrachtung mancher *single variations* hat die Einsicht eingebürgert, dass die Mutationen jedesmal bedeutende Veränderungen sein müssen, namentlich, dass sie grösser sein sollten als die Variationen.   Solches ist aber durchaus nicht der Fall, und anscheinend sind wenigstens zahlreiche Mutationen kleiner als die Unterscheide zwischen extremen Varianten."

If mutations cannot be recognized by their range of deviation, nor by their being inherited, from other variations which may chance to be unusually wide and to be hereditary, there is no test by which they can be recognized.   If a practical definition of a mutation had ever been framed, it could not have escaped De Vries; and if his idea could be formulated so that it would represent a distinct phenomenon recognizable as such in nature, he would certainly have given it that form.   I agree heartily with its friends in welcoming De Vries's work as the most valuable empirical contribution to our knowledge of the origin of novel forms of organisms since the *Origin of Species;* and that De Vries's method—the analysis of the composite character of a species into its elements, and the study of the origin (*and change*) of these—is far more rational and promising than the study of the "species," as we recognize them, as a whole.   But I regard his mutations as generically different from ordinary variations, and his specific characteristics as distinct and clear-cut in their existence and abrupt in origin, as undefined and not scientifically definable, because not representing distinct natural phenomena.

De Vries's recognition that the discontinuity of "discontinuous" variations does not necessarily distinguish them from "continuous"

variations is one of the best evidences of his familiarity·with the sub-
ject. Numerous writers ascribing to discontinuous variations the same
importance he does to mutations have, as he says, regarded them as
fundamentally distinct in the range of their deviation. Some of these
writers have regarded their importance as a function of the extent to
which they are aberrant. This question has been threshed over so
thoroughly that I do not care to touch on it more than to suggest again
the frequent sterility of sports. The assumed distinctness of discon-
tinuous variations is, however, by no means so trite a subject.

I disbelieve in the distinctness of these two classes of variations
on empirical ground, and *a priori*. We will consider the former first.
If they are distinct, it must be possible to draw a line between them,
and to say positively of any variation with which we are thoroughly
familiar that it is the one or the other, and to give a reason for the
judgment. It will be classed as discontinuous only when the series of
less considerable variations in the same direction breaks short of it.
But every first-hand worker in this field knows that such series always
tend to fill when the material is increased. In variation within wide
limits or limits approximately but not absolutely fixed, the extremes
of any finite number of examples are likely to be disconnected. When
the number is increased sufficiently the gaps fill up, but new isolated
extremes are found. Do the variations which are assimilated to the
regular curve in this way thereby become continuous? If "discon-
tinuous" means anything, they do; and if they do, it obviously does
not mean very much.

My abnormal ferns illustrate this assimilation of apparent mon-
strosities into a regular series with the accumulation of enough
material. The Polypodium I described from West Virginia, with the
apical segment and its neighbors greatly enlarged, seemed most
remarkable when I first collected it; but a thorough search of the spot
the next season showed a long series of specimens bridging the gap
between these seeming monstrosities and typical plants. I have had
the same experience with several lines of variation of *P. californicum*.
In its extreme form the caudate monstrosity, with the frond as a whole
narrowly oblanceolate, the individual segments abnormally broad and
widening toward the round or retuse apex, and the midrib springing
as a long curved hair from the dorsal surface, is the most extreme

freak fern I have ever seen.    From its occurrence in compact patches I am sure it is as near as nature comes to a mutation in DE VRIES's sense.    And yet, examining hundreds of specimens, I have found a very complete series of steps connecting it with typical plants.    Does the fact that thorough search fills the series class this freak outside of discontinuous variations, where it would unhesitatingly be placed if I had done less hunting?    What fern in the series is just aberrant enough so that if found alone it would constitute a mutation?    An answer should be possible if mutations and variations are distinct.

*Polypodium californicum* with its veins all free exhibits variation not merely beyond the limits of the species, but beyond those of the subgenus.[4]    That would be a mutation surely; but I have fronds of this kind and others with some anastomosing veins from the same rhizome; fronds with anastomosing veins on one side of the rachis and free on the other; and fronds with the two forms of venation variously distributed among the segments.    Among the fungi I have a number of examples of extra-generic variations, as the genera are now limited; but the boundaries are so artificial or dubious that most of these have no certain interest at present.    In a dozen or so American species of Puccinia, spores of the Uromyces type are common or at least known. In collections of Lenzites from a single log, I have specimens with many connected lamellae, and others with all of them free, which by themselves would unhesitatingly be referred to Agaricaceae, and still others strongly suggestive of Irpex.

It is hardly worth while to rehearse more instances in which mutations and ordinary variations cannot be distinguished; these few seem to me to prove the case as well as more would do it.    If mutations and variations were fundamentally different, it would be possible to say of any one of these peculiar ferns that it belongs in one or the other category, and the more copious the material the easier it would be to apply the classification; if it were but natural.    But the more thoroughly I have collected and examined them, the more evident it has become that the slight and extreme variations differ only in degree.    I am quite aware that this evidence is not of the same kind as DE VRIES's, and that his has a value in the study of heredity which mine absolutely lacks.

4 Goniophlebium was regarded as a distinct genus by BLUME, and is just now restored to that rank by UNDERWOOD.

My evidence is appropriate, however, to the question at issue.   Irrespective of the individual parentage of the plants, it shows that the distinction between wide and narrow, or continuous and discontinuous, variations is artificial.   That these aberrant forms should be the result of several generations tending in the same direction would be incomprehensible in view of the sterility of some of the forms and partial sterility of others; and would itself be contradictory to DE VRIES'S idea that new forms of plants arise suddenly, without preparation or intermediate steps.

The *a priori* objection to really discontinuous variation is the impossibility of really discontinuous development.   Every organism that varies grows, and varies only as it grows.   All organisms of any kind are indistinguishable during a considerable part of their development, but sooner or later their individual differences appear and become fixed.   The tendency of heredity, as the conservative factor in both evolution and development, we believe is to postpone the appearance of deviations from the parent types.   If they appear very late, the variations will be very small; if they appear earlier, they will obviously be more notable.   If variations in growth appear much earlier than usual, the variation will be unusually profound.   But it must be evident to anybody that it is not possible to select any point within the range of known deviation in the development of any organism whatever, and to say that the differences which occur before this time are different in kind from those which appear at and subsequent to it.

Variation, when it is just appearing, is a phenomenon involving small and homogeneous groups of cells; or, regarded in finer detail, single cells.   When variation occurs it is by the unit of the varying structure.   If it occurs early, the subsequent development of the units can make it become very conspicuous; but the variation *is* when it *is*, irrespective of later growth based on it.   Stomata and trichomes are as a rule formed late in development, and the presence of two where one is normal is likely to escape our attention, as is the presence of an extra leaf on a tree; cotyledons are formed earlier, and an extra cotyledon, perhaps involving an unusual form of the whole plant that grows from the seedling, is an object of interest and remark.   But when the first step toward the formation of the extra cotyledon was

taken it was certainly as small as can be imagined.   And surely there is no point between the formation of an extra cotyledon and that of an added leaf on a season's growth where mutations leave off and variations begin.   Both begin with the formation of two growing points from one.   Every step in growth is an insensible move from the preceding state; and variation, inexorably dependent on growth for its appearance, cannot be less continuous than growth is.

It may be objected to this argument that the variation does not occur in growth, but before it begins; say in the formation of the germ cells.   That cannot be demonstrated, even in as favorable subjects as the insects.   And if it were really and demonstrably true, it would not damage the argument, but merely shift it.   Life is an uninterrupted process from generation to generation.   The division of the chromosomes, the reduction in their number, and their combination in the sexual union are orderly, regular processes, just as the growth of any individual is.   In our ignorance of the forces at work and their way of working I can imagine no discontinuity in these finer, more recondite processes, any more than in more visible growth.   Nor can I see why we should regard differences between twin organisms as not arising in growth because we suppose their environment to be identical, and on that ground refer the differences which we certainly do see to still earlier stages in ontogeny, perhaps even antedating fertilization; unless we can show differences in the environment there.   It is perhaps natural to suppose that the things we do not understand happen in the stages we know least about, but this assumption does not share the nature of a proof.   It is therefore sophistry to plead that variations are independent of growth as an objection to the principle that they must be as continuous as growth is.

If variation is a phenomenon of growth, it may occur wherever growth is going on.   In the beginning of this paper I have pointed out that it actually does this in the oaks I studied.   It is as reasonable to speak of variation localized in the parts of a tree, each the product of the activity of an isolated meristem, as to regard the differences between parthenogenetically produced offspring of a single parent as examples of it.   KELLOGG has shown that variation is more considerable among the parthenogenetically than the bisexually produced members of a hive of bees.

## SUMMARY.

In this part of California, where conditions are locally very diverse, plants are more variable congenitally than in regions where the environment is uniform. For in the latter, natural selection acts along the same line on many generations, and the more closely plants breed true to forms fitted to their uniform environment, the better are their chances of perpetuation; while here natural selection is unlikely to work in the same way on many generations of variable plants; and breeding very close to a form fitted to any one sort of environment decreases the number of the plant's prospective descendants.

For the same reason, the ubiquists in this region are more variable than the plants of restricted occurrence. Their variation enables them to be ubiquists, and being ubiquists keeps them variable.

"Mutations," or discontinuous variations, and the most insignificant of individual variations are parts of one unbroken series.

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# KLINOSTATS AND CENTRIFUGES FOR PHYSIOLOGICAL RESEARCH.[1]

FREDERICK C. NEWCOMBE.

(WITH THREE FIGURES)

SOME years ago, when the author had to make use of the klinostat for extensive experimentation, the work went so slowly with one machine that means were sought to secure the operation of several klinostats at the same time without incurring the expense incident to the purchase of a number of the costly machines in common use. After some attempts to construct apparatus on too light and too cheap a scale, the apparatus here described was designed and manufactured with the cooperation of Mr. RALPH MILLER, at that time university mechanician. It has been used extensively for seven years, and has answered every demand made upon it. It is herewith described partly in response to several inquiries by men in other universities, and partly with the hope that it will be welcomed as offering a means for various kinds of research now practically impossible with the spring machines.

This apparatus can be provided with a horizontal and a vertical klinostat to run at the same time, the whole costing less than a Pfeffer machine; and the number of turn-tables can be increased almost indefinitely. Moreover, it will carry a much greater load than the spring klinostats.

## I. CENTRIFUGES.

For both the centrifuges and klinostats the same motive power is used—an electric or a water motor. I have found it convenient to have both kinds of motors; for while the electric motor runs more evenly and with less noise, the current is more liable to interruption from one cause or another. Should one have the advantage of a constant head of water, secured by a tank with constant water level, as suggested by ARTHUR,[2] a water motor alone would suffice.

[1] Contribution 83 from the botanical laboratory of the University of Michigan.

[2] ARTHUR, Water power for botanical apparatus. Proc. Indiana Acad. Sci. 1897: 156.

By a series of pulleys on shafts, as shown in *fig. 1*, any desired speed of revolution can be secured. In the figure two centrifuges are shown for revolution on a horizontal axis. The centrifuge nearer the motor shows a large chamber fastened to the revolving plate, as already described from this laboratory by REED,[3] while the centrifuge at the right carries a plate of ordinary size—about $15^{cm}$ in diameter.
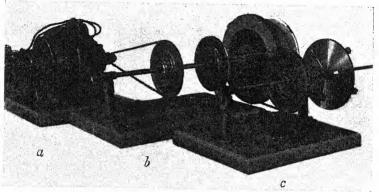


FIG. 1.—Electric motor (*a*) and two horizontal centrifuges (*b* and *c*).

## II.   THE KLINOSTATS.

The centrifuges of *fig. 1* are immediately turned into klinostats by the interposition of a worm reducing gear between the motor and the first shaft pulley. *Fig. 2* shows the apparatus set up for klinostat revolution; but in this figure, instead of the simple shafting with plate attached, as in *fig. 1*, we have a special form of klinostat shown, a form capable of revolution about either a vertical (*a*), a horizontal axis (*b*), or any oblique axis.

## III.   DESCRIPTIVE DETAILS.

The chief excellencies of this apparatus are found in what may be termed its unit construction, enabling an interchange of parts and an indefinite increase of turn-tables. The shafts are all the same diameter, the pulleys are interchangeable, and the shaft supports are all the same size.

[3] REED, A damp-chamber for use on the klinostat. Jour. Appl. Micros. **4**:1499. 1901.

*The motors.*—Instead of temporizing with cheap motors, it is better to purchase those of known efficiency at the outset. A one-fourth horse-power will do the work well. A constant water pressure or a constant electric current will demand only one motor. Neither of these sources of power being always constant at this university, I had to purchase both kinds of motors. The water motor is a Pelton $\frac{1}{4}$ HP with a water head of about $10^m$. The electric is a Sprague-Lundell pattern, $\frac{1}{4}$ HP. Both motors have a speed of 1,600 revolutions per minute.
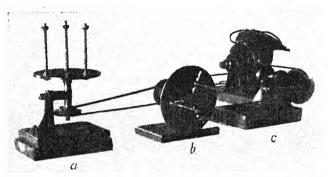


FIG. 2.—Two klinostats (*a* and *b*), the worm gear (*c*), and the electric motor back of the worm gear.

*The worm gear (fig. 3, a).*—As made by MILLER this reducing gear is manufactured in two sizes. In the smaller size the pulley worked by the worm has 100 teeth, thus reducing the speed to 0.01; in the larger size.the pulley has 200 teeth, thus reducing to 0.005. Besides this reduction caused by the worm, the pulley attached to the worm shaft and receiving the belt from the motor is four times the diameter of the pulley of the motor shaft. Thus the total reduction by the worm gear brings the 1,600 revolutions of the motor down to four times or two times per minute, according to the use of the pulley with the 100 teeth or 200 teeth. A revolution of four times per minute has been shown by CZAPEK[4] to bring in centrifugal action unless the plant is kept within $5^{cm}$ of the axis of revolution; and hence, for merely neutralizing the effect of gravitation, one should still further

4 CZAPEK, Untersuchungen über Geotropismus. Jahrb. Wiss. Bot. **27**:243. 1895.

reduce the speed from the smaller worm gear by interposing one of the step pulleys between the worm gear and the first klinostat. By the interposition of one such pulley, the speed of the first klinostat can be reduced to one revolution per minute, which is slow enough for objects less than one meter from the center of revolution. If desired, speed may be still farther reduced by other pulleys between the worm gear and the klinostat.
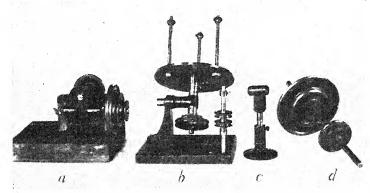
*The shafts (fig. 3, d).*—The shafts are of half-inch cold rolled steel, and are cut to any length.

*The shaft supports (fig. 3, c).*—These supports have a total minimum height of $12.5^{cm}$, and by raising the upper part of the support may be extended to a height of $15.5^{cm}$. This adjustment of the height of the support allows the shaft to be leveled up when the table or other object to which the supports are fastened is not level. The lower part of the support is a socket in which the stem of the upper part is held by a set-screw. The brass collar at the upper end of the support acts as a bearing, as shown in *fig. 1*, and automatically tilts up and down to conform to the direction of the shaft which passes through it. The middle piece of the support (*fig. 3, c*) has the shape of a tuning-fork, the stem of which is held in the socket below, and between the forks of which is received a plate projecting from the lower side of the collar above. An iron pin passing through the arms of the fork and the plate of the collar suspends and hinges the collar, and thus allows the automatic tilting. The three movements allowed the upper part of the support—that of vertical movement in the socket, rotation in the socket, and tilting of the collar—give ready adjustment to all possible faults of mounting of the shafts, prevent all binding, and have much to do with the easy running of the machines.

*The pulleys (fig. 3, d).*—The pulleys for the horizontal shafts are of cast iron, and made with three steps of 4, 8.5, and $15^{cm}$ diameter respectively. Each step has a peripheral thickness of $1^{cm}$ and has turned in it a V-shaped groove to take a quarter-inch leather belt. The pulleys are fastened to the shafts by set-screws.

*Special turn-tables (fig. 2, a and b; fig. 3, b).*—The foregoing apparatus is sufficient for centrifuges and klinostats revolving with horizontal axis. For revolution about a vertical axis the machines shown in the figures referred to have been made. They have an iron

base $20 \times 14 \times 2.5^{cm}$.  An iron support screwed to this base rises
vertically and carries at its upper end a horizontal arm which holds
a collar through which passes the half-inch shaft of the machine.
One end of this shaft, as shown in the figures, receives a brass two-
step pulley, and the other end the usual plate for supporting the
object under experiment.  This plate is of heavy brass $15-20^{cm}$ in
diameter, and has cut in it three equidistant radial slots which
receive the ends of brass posts.  The brass posts have shoulders
which rest upon the brass plate on the upper side (*fig. 2, a*), while
nuts on the opposite side secure the posts at any desired distance from



.Fɪɢ. 3.—Worm gear (*a*), turn-table (*b*), shaft standard (*c*), and shaft and
pulleys (*d*).

the center.  The free ends of the posts have a thread on which runs
a nut to be screwed down over the edge of a flower-pot or other con-
tainer.

The horizontal arm projecting from the support rising from the
base is held against the vertical support by a heavy friction screw
passing through the vertical support and into the horizontal arm.
This friction screw is turned by a removable steel rod passing through
the head of the screw.  By manipulating the friction screw, this
machine may be set with its shaft at any angle desired, allowing the
same klinostat to be used for revolution about a vertical, horizontal,
or oblique axis (*fig. 2, a and b*).

*Idler pulleys and support.*—For adjusting the klinostats to cramped positions, or to fixed directions of light, it is often desired to turn a driving-belt from a straight course. This has been accomplished by means of the shaft and two small pulleys shown standing in the right-hand end of the klinostat base in *fig. 3, b*. This position of these idlers is right for the klinostat to which they are shown attached when the klinostat is adjusted for revolution with horizontal axis. For other purposes I have had made a cheap iron-base into which the pulley shaft is set, and this device allows a belt to be turned at right or oblique angles anywhere desired.

*Belting and couplings.*—The belts used are of one-fourth inch leather. The thimble-like couplings screw over the ends of the belt and hook into one another. Both belting and couplings are common articles of trade.

*Shaft-stops.*—It is often desirable to keep a shaft from working out of some position in which it is placed or to prevent it being accidentally pushed out of position and thus destroying the alignment of the pulleys. For this purpose several collars are cut from half-inch brass tubing, and each collar is provided with a set-screw. Two such collars are shown one above and one below the small pulleys on the vertical shaft rising from the base of the klinostat (*fig. 3, b*).

Besides what has been already mentioned there are several things which might be added in commendation of this apparatus. It is easily portable, in spite of its seeming size. The parts may all be screwed to a movable table, or each part may be screwed to a piece of plank and the parts then clamped to tables. The shaft supports and bearings are easily shifted, placed nearer together or farther apart, so that one may use many shafts of various lengths with any two supports. One end of a horizontal shaft may be made to project any desired distance beyond a support, and the free end of the shaft may support a klinostat or centrifuge plate, thus allowing the plants used to be pushed into the recess of a window or into a small, closed chamber. The pulleys can be shifted to any position on the shafts, or any number of pulleys attached to a single shaft, thus allowing the turn-table driven by that shaft a variety of positions, or allowing several turn-tables to be driven from one shaft. The speed of revolution can anywhere be increased or diminished, and a variety of

speeds can be otained from the same shaft at the same time by belting to larger or smaller steps on the pulleys.

A machine, however simple and however powerful, is of little use unless it will accomplish the purpose of its design. A klinostat, as is well known, must move through any quadrant in the same time it traverses its counter-quadrant. The experience of years has demonstrated that the apparatus here described is not faulty in this particular. Of course, the loads must be balanced, and this is done as on any klinostat. There is no danger from the creeping or stretching of the belts. The unevenness of motion imparted by a water-motor attached to a central system seems to have no effect in causing either heliotropic or geotropic curves on the klinostats, the irregularities of one minute apparently correcting those of another, since the irregularities are not periodic.

*Cost.*—The minimum cost for a complete unit of this apparatus may be given thus:

| | | |
|---|---|---|
| 1 ¼HP electric motor with rheostat - - - - - | | $35.00 |
| 1 ¼HP water motor - - - - - - - | $24.00 | |
| 1 worm gear - - - - - - - - - | 12.50 | 12.50 |
| 2 shaft supports - - - - - - - - | 2.50 | 2.50 |
| 2 ft. ½ in. steel shaft - - - - - - - | .12 | .12 |
| 1 3-step pulley - - - - - - - - | 1.50 | 1.50 |
| 1 klinostat (*fig. 2, a* and *b*) revolving on either vertical or | | |
|     horizontal shaft - - - - - - - - | 9.00 | 9.00 |
|     Total cost - - - - - - - - | $49.62 | or $60.62 |

The equipment contained in this list provides a centrifuge with horizontal axis, revolving 800, 400, 200, 100 times per minute, and almost any lower speed, and with a klinostat revolving on either a vertical or horizontal axis with speeds from the centrifuge rate down to one revolution in four minutes. Moreover, it allows one centrifuge and one klinostat to be operated at the same time, or two centrifuges to be operated at the same time.

Additional centrifuges or klinostats with horizontal axis can be obtained tor $6 each, and with vertical axis for $9 each.

When one considers that the standard spring klinostats with but one turn-table cost $60 to $80, it can be seen that for the same expen-

diture the apparatus described in this paper possesses many times the efficiency of those, not counting cost of power.

Should anyone desire to construct this apparatus, I shall be willing to give additional details; or I will gratuitously supervise the construction should any one wish to have the work done by Mr. Miller. In the latter case, application for construction should be made to Messrs. Eberbach & Son, Ann Arbor, Mich., into whose employ Mr. Miller has entered.

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# ECOLOGICAL NOTES ON THE TREES OF THE BOTANICAL GARDEN AT NAPLES.

GRACE E. COOLEY.

(WITH FOUR FIGURES)

A VIEW of the country about the bay of Naples in the spring gives very little idea of the luxuriance of the vegetation of which the land is capable. The only trees left standing are the stone pines, and these are pruned to the very crown for firewood, leaving only the upper cone-bearing branches, which produce the seed the people so much enjoy. The ilex oaks never get much higher than the rosemary and the heather, and all are lopped for fagots, unless they have selected inaccessible rock niches to grow in. To be sure, the peasants cultivate the black poplars, but only for use in their vineyards. The living trees make the vine posts, and the cut branches of their pollarded trunks are used for stakes and cross-bars for the clinging tendrils. Every winter the shoots are cut back from the top of the trunk, and every summer a small new crop grows from the mutilated top, making a light shade from the hot rays of the sun.

It is a singularly treeless region. The impression of the country in the clear atmosphere is much like that of the foothills east of the Cascades in the rainless regions of Washington and Oregon. There is the same soft gray color on the hills, that readily changes under the influence of the sun and the clouds, and the gray artemisias on the rocks help to make the picture the same. Yet this land, so like our own desert in color and absence of trees, is very different in its power to produce the fruits of the soil. There is water to be had from the clouds in abundance at all seasons, except in the three summer months, and the apparent barrenness is only the result of the kind of crops the peasant plants, and the way he has dealt with the native trees. Every available spot is devoted to the cultivation of the grape, and the land is terraced for vines up the slopes of the old volcanic cones and sometimes down to the very depths of their worn-

out craters. All the wild shrubs go into the fire to cook the daily meal. The succulent cactus and the spiny century plant, fugitives from America, are protected from the hacking of the peasant's knife, and having escaped have made themselves perfectly at home here.

It is only in the gardens that one sees trees, and there one is struck by the cosmopolitan mixture. There are few natives of Italy, but many foreigners. The ilex oak is the hardiest of the natives, and the tree most often used along the avenues in the parks, but, with this exception and the cypresses and Judas trees, the gardeners have gone to other countries to get trees for adornment. A critical eye is at once struck by the multitude of plant types represented, and the marvel grows when one considers the exact habitat of the foreigners and the perfection of their development under cultivation here in Italy. This Mediterranean region is the home of the *Hartlaubgehölze* of the warm temperate zone, with the ilex oak, European olive, and classic laurel among the best-known and most representative examples; but there are Australian trees here from within the tropics; trees from the cold northern forests of our own land; some from the deserts of Africa; and others from the mountains of Asia. They stand for types of all the ecological regions of SCHIMPER, except the Arctic and the ever rainy forests of the tropics. The soil and the climatic conditions seem remarkably congenial to these strangers, and they appear to grow as well as under the conditions native to them.

The Royal Botanical Garden of Naples is an admirable place for the study of diverse types of trees, for it furnishes many species and these are growing almost in a state of nature. The funds of the garden have been for many years too small to give them much care beyond that which locks the gates and gives them the chance to live. The whole yearly allowance for the support of the gardens, the greenhouses, the library, and all the force employed from the director to the gate-keeper is 7000 lire (about $1400). Some years ago there was sometimes a little to be expected from the city of Naples, but the sum has been for many years too inadequate for what we should consider the actual needs of a botanical garden. One resident spoke of it as "a ruin twenty years ago," but the very ruin is of deepest interest to a student of ecology. It shows forms from many climates mingling

and growing freely under conditions unnatural to them at home, and the marvel is that they find it so easy to do it.

It is instructive to run over the climatic conditions that exist here and contrast them with what can be gathered concerning those of other lands which have representatives here.    Naples lies in the warm temperature region of winter rains.   The latitude is 40° 52′, the longitude 14° 15′ east.   The garden is a short distance from the sea, from 31.30 to 44.50$^m$ above it, and lies on a slope that looks southeast to Vesuvius.    Back of it and protecting it from the north winds, rises the hill of Capodimonte, on which is an observatory from which the meteorological observations were taken which are given in the table below.   Since the hill is much higher than the garden and more exposed, the conditions are not quite those which hold in the garden itself, 103$^m$ below.   In an account of the garden published in 1867 by Pasquale, a former director, some of the climatic conditions are discussed.   In 1846 there was a summary made of the observations of temperature for twenty-four years.   The medium temperature for these years was 15.66° C.   The highest temperature recorded was for July 17, 1841, 39° C.; the lowest was February 21, 1845, −5.8° C. The period of greatest heat succeeds July 25, and that of greatest cold January 24.   Specially cold nights are recorded, when the temperature sank to −7° C. and −8° C.   Such periods of extreme cold are rare, occurring perhaps only once in ten years.   The thermometer seldom sinks to the freezing-point, and hoar frosts are most unusual.   The table given below is for the year 1902, and is taken from the monthly reports published by the observatory of Capodimonte, 149$^m$ above sea-level.

The rain falls for the most part in the winter, but the amount that falls in special months varies from year to year.    In general it is greatest from October to February, and least in June, July, and August; in 1902 sinking to zero in July.

Schimper divides the globe into regions according to the relative amounts of rain during the year and the seasons in which it falls. If we follow this classification in arranging the plants of the garden, grouping them with the countries where they are native, we shall be able to make some interesting comparisons.

METEOROLOGICAL OBSERVATIONS TAKEN AT CAPODIMONTE FOR THE
YEAR 1902

| Months | Average of maximum daily temperature ° C. | Average of minimum daily temperature ° C. | Average of relative humidity at 3 P. M. | Total rainfall in mm. | Evaporation in the 24 hours in mm. | Maximum temperature ° C. | Minimum temperature ° C. |
|---|---|---|---|---|---|---|---|
| January.............. | 11.88 | 7.23 | 62.8 | 65.6 | 44.8 | .... | 0.8° |
| February............ | 13.32 | 8.66 | 76.6 | 103.4 | 34.1 | 16.9° | 4.1 |
| March............... | 14.12 | 8.19 | 68.7 | 76.1 | 56.9 | 17.5 | 2.4 |
| April................ | 18.79 | 12.26 | 71.6 | 65.8 | 55.6 | 21.7 | 6.5 |
| May................. | 18.35 | 11.42 | 55.3 | 80.2 | 70.3 | 26.3 | 8.0 |
| June................ | 23.99 | 16.59 | 55.0 | 8.0 | 107.0 | 29.7 | 11.0 |
| July ................ | 28.73 | 20.50 | 61.1 | 0.0 | 137.7 | 31.3 | 17.8 |
| August ............. | 28.66 | 20.29 | 62.7 | 9.0 | 110.5 | 33.6 | 16.0 |
| September........... | 26.14 | 18.98 | 64.3 | 82.5 | 102.1 | 32 | 13.6 |
| October............. | 20.34 | 15.41 | 78.7 | 171.7 | 59.8 | 26.3 | 10.2 |
| November........... | 14.98 | 9.80 | 70.8 | 157.8 | 47.0 | 18.5 | 5.3 |
| December .......... | 11.23 | 6.91 | 67.8 | 66.9 | 46.3 | .... | 2.1 |
|  |  |  |  | 887.0 |  |  |  |

1. *The temperate regions of winter rains and summer drouths.*—
The countries included are Italy and the other lands bordering on
the Mediterranean, the coast of southern California, and the coast
region of southwestern Australia. These regions are in about the
same latitude, and they all have an annual rainfall of 60–130$^{cm}$.
Representatives in the garden are many, the ones selected for our
purpose being as follows: ITALY: Quercus Ilex, Olea europaca,
Laurus nobilis, Pinus Pinea, Cupressus sempervirens; GREECE to
PERSIA and AFGHANISTAN: Pinus brutia; ASIA MINOR: Cedrus
Libani; SOUTHWESTERN AUSTRALIA: Eucalyptus and Acacia; PACIFIC
COAST OF SOUTHERN CALIFORNIA: Libocedrus decurrens, Chamae-
cyparis Lawsoniana, Cupressus macrocarpa, Pinus sabiniana, Sequoia
sempervirens.

2. *The regions of heaviest rain in spring and early summer and
the beginning of winter, with drouths in late summer.*—Included in
this group are the greater parts of Spain, France, Switzerland, and
Austria. The annual rainfall varies in these countries from 60 to
over 130$^{cm}$. It will suffice to give only one or two examples from the
many that could be given: Larix europaea, Fagus sylvatica, Quercus
Suber, Pinus pyrenaica, Abies Pinsapo.

3. *The regions where all the months of the year are rainy or snowy.*—
Included in this class are northern Europe, parts of Siberia and the

extreme north of Japan, North America on the east from Hudson Bay throughout the Alleghanies and on the west as far south as British Columbia. The range of latitude is from 30° northward; and the annual rainfall is 60–200$^{cm}$. EUROPE: Picea excelsa, Pinus sylvestris; SIBERIA, AMOOR REGION, and NORTHERN JAPAN: Abies firma, Cryptomeria japonica; WEST COAST OF AMERICA: Chamaecyparis nutkaensis; ALLEGHANY REGION: Pinus Strobus, Liriodendron tulipifera, Prunus serotina, Robinia pseudacacia, Celtis occidentalis, Tilia heterophylla, Gleditschia triacantha, Quercus nigra.

4. *The regions of winter rain or snow and heavy summer rains.*— Countries included in this group are British Columbia, Central Japan, and parts of Chile. The range of latitude is 40°–50°, and the annual rainfall is 130 to over 200$^{cm}$. Examples of these regions are as follows: BRITISH COLUMBIA: Chamaecyparis nutkaensis; CHILE: Araucaria imbricata; CENTRAL JAPAN: Chamaecyparis pisifera, Torreya nucifera.

5. *All the months of the year rainy, the most in winter, but no month without fifteen rainy days.*—The southern part of New Zealand is the only region where this condition holds. No trees of the garden are surely from this region, unless possibly a Dacrydium sp.

6. *All the months of the year rainless, at least with less than six days of rain.*—Under this group come the deserts of the Sahara, central Asia, central Australia, Arizona, and southern California. The latitude range is 20°–50°. This region is that of least rain, never more than 60$^{cm}$ falling annually. OASES OF THE SAHARA: Phoenix dactylifera; GOBI: Tamarix articulata; ARIZONA: tree yuccas and agaves.

7. *Regions of the normal rainy season of the tropics and subtropics, with some drouth in winter and spring.*—The countries included are China, Japan, India, the East Indies, New Guinea, eastern Australia, southern Florida, the Mexican plateau, the West Indies, Central America, Peru, Brazil, and Argentine Republic. This region includes the monsoon forests of India and Brazil, where the annual rainfall exceeds 200$^{cm}$, the latitude ranging from the equator to 40°. The trees selected from the garden to represent this region are as follows: CHINA: Camphora officinalis, Ginkgo biloba, Cephalotaxus Fortunei, Chamaerops excelsa, Livistona chinensis; JAPAN:

magnolias and camellias; INDIA: Pinus excelsa (found also in an isolated area on a height in Greece), Acer oblongum, Corypha australis; NEW GUINEA, AUSTRALIA, and NEW ZEALAND: Araucaria Bidwellii, A. Cunninghamii, Melaleuca styphelioides, Calistemon saligneum alba, Grevillea robusta; SANDWICH ISLANDS: Pritchardia pacifica; BRAZIL and the ARGENTINE: Eugenia Michelii, Araucaria brasiliensis, Prosopis torquata; ANDES, PERU, BOLIVIA: Schinus molle, Phytolacca dioica; MEXICO: Pinus Montezumae, P. patula, Taxodium mucronatum, yuccas and agaves in regions of less rain; WEST INDIES: Cordia martinicensis; FLORIDA and the ADJACENT GULF STATES: Sabal Adansoni, Magnolia grandiflora, Planera aquatica, Liquidambar styraciflua, Torreya taxifolia, Persea Borbonia.

The plants chosen from the large number in the garden to represent the above regions have been selected particularly because they are well known as types of peculiarly significant societies. Another consideration, which is also a limitation, has restricted the examples to certain groups, such as the conifers and palms, because it has been impossible in many other cases to secure data as to the exact climatic conditions under which the trees are found in a natural state. Information of an exact nature in reference to this is most meager, as everyone knows who has consulted floras to find the ranges of species or the habits of plants with regard to environment. No plants were placed in the list which do not seem to be reasonably vigorous, and many of them are growing most vigorously, as will be seen by the following measurements of circumference taken $30^{cm}$ from the ground: *Pinus excelsa* $297^{cm}$, *Camphora officinalis* $278^{cm}$ (spread of horizontal branches $12^m$), *Taxodium mucronatum* $258^{cm}$, *Sequoia sempervirens* $239^{cm}$, *Cedrus Libani* $227^{cm}$, *Araucaria Bidwellii* $195^{cm}$, *Ginkgo biloba* $191^{cm}$, *Chamaecyparis Lawsoniana* $172^{cm}$.

The classification shows that the garden represents plants from $61°$ north latitude to $48°$ south latitude. Countries are represented with an annual rainfall of 20 to more than $220^{cm}$. There are plants from the high mountains, the Canary pine growing at $2000^m$; *Pinus excelsa* has a range on the Himalayas of 1800 to $3200^m$; *Taxodium mucronatum* grows on the highlands of Mexico from 1600 to $2300^m$; and *Pinus Montezumae* from 2500 to $4400^m$ on Orizaba. There are

plants that thrive in swamps and those that grow in rocky or sandy places.   Few regions of the whole earth have not here their representatives.

Still more impressive than these plain facts is a walk in the garden itself in early spring, when the great variety of foliage shows itself to perfection.   There is a yellow-green just appearing in the deciduous oaks and maples in the midst of the jungle of tropical evergreen trees with their glossy dark green foliage, and in sharp contrast to both are the gray phyllodial leaves of the Australian wattles, and such plants as *Colletia cruciata*, or the thin gray foliage of the lofty melaleucas and eucalyptus trees.   Tree yuccas and tall dracaenas thrust their swordlike leaves through the soft sprays of the conifers.   The date palms grow here vigorously and sometimes show a curious adornment of climbing ivies, while northern ferns and blossoming herbs grow in the axils of their fallen leaves.   One such palm on close observation showed a score of young seedling maples that had taken root on the trunk of the tree, and had already passed their first summer successfully.   Beside the maples, there were on the same tree trunk raspberries, grasses, geraniums, *Cotyledon umbilicus*, fumitory, masterwort, and perennial ferns, forming a most friendly and thriving community.

On superficial view of the trees there seems little variation from normal habit, but there is one tendency so strongly developed here that it seems to be climatic.   Many trees develop root-shoots and sprouts from the old wood of the trunks.   This is conspicuous in the conifers and palms, where it is certainly an exception to the usual habit of the groups.   *Chamaecyparis Lawsoniana* has, besides the main trunk, four prominent ones given off just at the ground line, and they are conspicuously large and well-developed, the main trunk being $172^{cm}$ in circumference, and the others 56, 45, 40, and $40^{cm}$.

*Araucaria Cunninghamia* has four bushy shoots about $90^{cm}$ from the base of the trunk.   Some specimens of *Pinus canariensis* are clothed to the ground with filmy shoots, recalling the habit of many American elms (*fig. 1*).   No other pine with which I am familiar has this habit except *P. rigida*, which frequently exhibits it in regions subject to forest fires.

One specimen of *Cryptomeria japonica* has a remarkable habit

of producing branches some distance from the ground which bend down, and when they meet the soil broaden out and root, throwing up erect stems which become independent trees. The tree is $110^{cm}$ in circumference and has given rise to six such independent growths, one $65^{cm}$ in circumference; the others 45, 30, 27.5, 12.5, and



FIG. 1.—*Pinus canariensis:* trunk clothed to the ground with shoots.



FIG. 2.—*Cryptomeria japonica*, showing one of five daughter trees from suckers; two suckers in view.

$12.5^{cm}$, all $30^{cm}$ from the ground. The highest of such rooting branches is given off from the trunk $60^{cm}$ above its base. It is $8.75^{cm}$ in circumference until it touches the ground, where it flattens and broadens to $15^{cm}$ in surface view, and creeps some distance from the trunk before rising into the erect shoot. *Fig. 2* shows only one of the daughter trees and two of the suckers.

Several specimens of *Phoenix dactylifera* in the garden produce

leafy shoots in the axils of the old leaves near the base of the trunk, and even some distance from the ground. A very remarkable case of this kind is shown in *fig. 3*, a photograph of a palm growing in a private garden in Naples. Twenty leafy shoots were counted on one side of the trunk alone. The trunk just above the soil measures
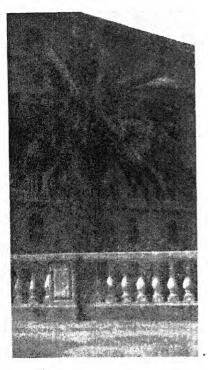


FIG. 3.—*Phoenix dactylifera*, with leafy shoots in the axils of old leaves.

FIG. 4.—*Phoenix dactylifera*; companion tree to that shown in *fig. 3*, whose leaves show in the upper foreground.

$257^{cm}$ in circumference, but these abnormal growths so increase its size at a height of $130^{cm}$ that it measures $500^{cm}$. In this tree and on the others in the botanical garden roots had arisen from the base of these shoots, but after growing a few centimeters they had died. *Fig. 4* shows the companion tree to the date palm of *fig. 3*, which has followed its natural habit. The branching one has not attained the height of the other, but is well developed in every other way.

*Chamaerops humilis*, the low native palm of the Mediterranean coasts, grows here into a thick bushy tangle from the development of an immense number of underground shoots. This is not an uncommon habit of the plant when growing wild in northern Africa. *Phytolacca dioica* has a curious flat table-like formation of its main roots or of the lower stem just above the ground line, and from this spring a great number of slender vigorous shoots.

The trees of the garden are not of great age, for the garden itself in its present foundation is not very old. Although as early as 1662 there was here a pharmaceutical garden connected with one of the church hospitals, in its present state it was founded in 1809 under the auspices of the Bourbon rulers. Its first director was MICHELE TENORE, who held the position for fifty years. He was succeeded by GUGLIELMO CASPARRI (1861–1866) and GIUSEPPE ANTONIO PASQUALE (1866–1867). In 1893 FREDIRIGO DELPINO, formerly in Genoa and Bologna, became its director, and he still holds the position. TENORE in his long term of fifty years put in train the plans which have been largely followed since. The important large trees now in the garden are included in a catalogue published in 1867 by PASQUALE. In many cases he gives the heights of the tallest trees, and from his figures we can judge that the growth since that time has been strong and normal. With a few exceptions the trees are probably none of them much older than one hundred years. A few of them have been broken by tempests and one or two are stag-headed, but most of them show no signs of abnormal growth. They are not well pruned, but in a natural woodland condition that is most interesting.

It is a remarkable collection when one considers how little care has been given it. One marvels at the friendliness of the climate which has proved congenial to so many strangers. In our own country southern California has a somewhat similar type of native vegetation and somewhat similar climatic conditions, but even there it would hardly be safe to leave such a collection of trees to themselves. One feature of importance is the great fertility of the soil in this region, which has been under the influence of civilization for three thousand years, and probably a good part of that time under cultivation, yet it still yields several harvests a year.

Such a climate as this would be an ideal one in which to establish an experimental garden, with the study of variation in structure in special view. The garden already contains valuable material for research. Naples has proved to be a splendid situation for the Marine Biological Laboratory. There is a place here also for a great botanical station for the study of plants from all the world. The botanists have left the ecology of this region almost untouched until lately, and now Professor J. Y. BERGEN is working on the plants of the Solfatara. This pioneer work should indicate the possibilities of this region as a place where the American botanists might establish a station which would do for botany what the German zoologists have done for zoology.

STAZIONE ZOOLOGICA,
    Naples.

# RELATIVE TRANSPIRATION OF OLD AND NEW LEAVES OF THE MYRTUS TYPE.

### JOSEPH Y. BERGEN.

WHILE making some studies of the transpiration of the coriaceous-leaved evergreens of the Neapolitan region, such as *Olea*, *Pistacia*, and *Quercus Ilex*, the writer became interested in the question of the relative activity in transpiration of their old and new leaves. Some results of the measurements made upon them are here set down, together with a few words of discussion in regard to the meaning of the facts observed.

It is commonly said that the trees and shrubs of the Mediterranean region are largely evergreen, but a little examination into their characteristics shows that the word "evergreen" should be used to describe them only when its meaning is carefully defined. When local floras, like GUSSONE's excellent catalogue of the plants of Ischia, describe such summer deciduous shrubs as *Spartium junceum*, *Cytisus scoparius*, and *Calycotome villosa* as evergreens, it would seem that any woody plant with leaves which remain green during a considerable part of the winter is considered to be an evergreen. As a matter of fact, the angiospermous trees and shrubs of the coastwise region about Naples seem to be classifiable, as regards their mode of shedding the leaves, into the divisions shown in the table[1] on the opposite page.

Some of the plants of division I may be described as facultative deciduous species; that is, they may retain their leaves almost or quite the year around. The Medicago and the Euphorbia above named do this when the water supply is abundant.

The members of division II are more or less covered with leaves at all seasons. Those which belong to subdivision 1 show little difference in density of foliage dependent on the season. Many, however, of subdivision 2 lose nearly all their old leaves soon after the new leaves have reached their full size (area). *Rhamnus Alater-*

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[1] The table given is merely illustrative and does not embrace nearly all the species which the writer has observed.

| | | |
|---|---|---|
| I. Leaves simultaneously deciduous | 1. Winter deciduous | *Juglans, Populus, Fagus, Castanea, Quercus*(in part),*Ulmus, Morus, Ficus, Vitis,* etc. |
| | 2. Summer deciduous | *Calycotome villosa*<br>*Coronilla Emerus*<br>*Spartium junceum*<br>*Medicago arborescens*<br>*Euphorbia dendroides* |
| I. Leaves not simultaneously deciduous (evergreen) | 1. Leave some of them lasting two years or more | *Olea europaea*<br>*Pistacia Lentiscus* |
| | 2. Leaves lasting more than one year but less than two | *Rhamnus Alaternus*[2]<br>*Nerium Oleander*[2]<br>*Quercus Ilex*[3]<br>*Ceratonia Siliqua*[3]<br>*Arbutus Unedo*[3] |

*nus* and *Nerium Oleander* are therefore much less leafy by July 1 than they were throughout May.

A large proportion of the time spent was devoted to leaves of the so-called Myrtus type; those namely of *Olea europaea, Quercus Ilex, Rhamnus Alaternus,* and *Nerium Oleander.*

Four other species, namely, *Pistacia Lentiscus, Hedera Helix, Smilax aspera,* and *Viburnum Tinus,* were also studied, in order to give any conclusions that were reached a more general value, as applicable to the sclerophyll trees and shrubs of the region.

With every species, some comparisons of the relative rate of transpiration for old and new leaves were made as soon as the latter had reached their full areal growth.

### RELATIVE THICKNESS OF OLD AND NEW LEAVES.

On comparing the thickness of the old leaves with that of new ones of the same species which had just reached their full area (usually in May) the older ones were commonly found to be somewhat thicker. All of the species in the list above given were examined except Viburnum, and the average ratio for all seven species was $\frac{\text{thickness old leaf}}{\text{thickness new leaf}} = 1.2$. The greatest disparity was found in Pistacia, which sometimes gave a ratio of 1.48, and the least was in Hedera, which frequently showed no difference in the respective thicknesses. The greater thickness of the old leaves was not mainly due to growth of the

[2] These last fifteen months or but little more.   [3] These last eighteen months or more.

epidermis; the amount due to this cause was never found to be more than 10 per cent. of the whole difference in thickness, and sometimes the epidermis of the new leaf was as thick as that of the old one.    All the measurements were carefully made with the eye-piece micrometer.

### RELATIVE TRANSPIRATION OF OLD AND NEW LEAVES.

The measurements of transpiration were all made by determination of loss of weight of twigs in water, except in the case of Nerium of which leaves only were used, with the petioles immersed.    The time allowed was usually one hour, and the temperature (always the same for each comparison) ranged on different days from 25 to 31° C. Observations were begun on May 8 and continued at intervals until August 6.

In the following table are given the ratios of rates of transpiration for equal areas of old leaves and new ones which had just attained the'r maximum area.    The values given are usually averages of several observations taken daily or at intervals of two or three days during a period of a week or ten days.    The column $o \div n$ represents the ratio, *amount of transpiration per hour for* $100^{sq\,cm}$ *of old leaves divided by the corresponding amount for new leaves.* .

TRANSPIRATION RATIOS; EQUAL AREAS.

| | $o \div n$ |
|---|---|
| *Olea europaea* - - - - - - | 1.05 |
| *Quercus Ilex* - - - - - - | 3.53 |
| *Rhamnus Alaternus* - - - - - | 0.78 |
| *Nerium Oleander* - - - - - | 2.45 |
| *Pistacia Lentiscus* - - - - - | 1.08 |
| *Hedera Helix* - - - - - - | 0.18 |
| *Smilax aspera* - - - - - - | 2.16 |
| *Viburnum Tinus* - - - - - | 2.10 |

It is obvious at a glance that in general the new leaves have not attained their full power of transpiration when they have reached the area of maturity.    This fact is not wholly a result of the imperfect development in thickness already mentioned, for when the transpiration ratios are referred, not to equal areas of leaves, but to equal weights, the older leaves often maintain their position as the more active, as is sufficiently shown by the following values.    These results cannot be closely compared with those of the preceding table, since

the former contains averages based on a larger number of determinations for each species.

TRANSPIRATION RATIOS; EQUAL WEIGHTS.

|  | $o \div n$ |
|---|---|
| *Quercus Ilex* - - - - - - | 2.73 |
| *Smilax aspera* - - - - - | 2.32 |
| *Viburnum Tinus* - - - - - | 1.74 |

In two species, the Rhamnus and the Hedera, the old leaves are seen to be notably deficient in capacity for transpiration. In the former this fact is very possibly due to the moribund condition of the old leaves, which at the time of observation were about to turn yellow and fall. In the latter, the leaves were not ready to fall, and some other explanation of their sluggish action needs to be sought.

In view of the marked differences in transpiration between the old and the new leaves of most of the species studied, it seemed worth while to investigate the question whether these differences were accentuated or diminished by covering the stomatal surface (the lower one) with wax and so comparing the normal transpiration with the epidermal taken alone. This inquiry was not undertaken until so late in the season that only a portion of the comparisons which it would have been desirable to make were possible. The most convenient way of expressing the results seemed to be to give the ratio, *loss of water by plain leaf divided by loss of water by waxed leaf*, first for the old leaves, then for the new ones, of each species examined.

TRANSPIRATION RATIOS; PLAIN AND WAXED LEAVES

|  | PLAIN $\div$ WAXED | |
|---|---|---|
|  | Old leaves | New leaves |
| *Olea europaea* | 2.62 | 3.17 |
| *Nerium Oleander* | 3.52 | 12.75 |
| *Pistacia Lentiscus* | 3.00 | 5.33 |
| *Hedera Helix* | 2.93 | 6.80 |

In the species examined it is evident that the total transpiration exceeds the epidermal alone much more in the new leaves than the old ones. Examination of the actual amounts of moisture lost in each case leads me to suppose that this inequality is due to the

greater impermeability of young epidermis (several months old) than of that which is more than a year old, and to the greater functional activity of the younger than of the older stomata. One would *a priori* have expected to find the thicker and more indurated epidermis of the older leaves more impermeable than that of the younger ones, but in many cases it certainly is not. For instance, the older leaves of Nerium were found to lose moisture more than five times as fast for equal areas as the younger ones (both with the lower surface waxed), and the older leaves of Olea lost moisture nearly four times as fast as the younger ones (both waxed below).

In the table above given the losses from waxed leaves may be a little too high relatively to the losses from plain leaves, since the former values were obtained after the leaves had been standing in water longer, and therefore, perhaps may have established a better transpiration current. But this would not affect the general conclusions to be derived from the data.

The leaves of Olea and of Pistacia compared in the last table were aged about six months ("young") and eighteen months ("old") respectively, and those of Nerium and Hedera were about three and a half and fifteen and a half months of age.

None of the results obtained by the writer in transpiration experiments upon sclerophyll leaves can be much elucidated by comparison with the conclusions (contradictory among themselves) obtained in the studies of young and old leaves by SCHIRMER, KRUTITZKY, TSCHAPLOWITZ, HÖHNEL, and others,[4] since none of these authors dealt with leaves which differed in age by an entire year. It is also unlikely that sclerophyll leaves should in their behavior as regards transpiration closely resemble the leaves of the herbaceous Gramineae, those of Coleus, Phaseolus, Pisum, and such other species as have received most study with reference to the relation between their development and their power of transpiration.

### CONCLUSIONS.

The conclusions of the present paper may be summarized as follows:

1. The evergreen trees and shrubs of the Neapolitan region differ greatly in the longevity of their leaves, some of the species having

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[4] Summarized by BURGENSTEIN, Materialien zu einer Monographie betreffend die Erscheinungen der Transpiration der Pflanzen. II Theil, pp. 25, 26. Wien. 1889. A. Hölder.

leaves that live only about fifteen months, while those of others live more than two and a half years.

2. All of the leaves studied reach their maximum area considerably before they attain their full thickness.

3. The leaves of six out of the eight species studied transpire more for equal areas when fifteen to eighteen months old than they do when they have just reached their maximum area (*i. e.*, at three or four months).

4. Transpiration for equal weights of leaves is generally more active for leaves of fifteen or more months than for those of three months or a little older.

5. Epidermal transpiration bears a much smaller ratio to total transpiration in leaves of three months than in those of fifteen months.

NAPLES, ITALY.

# REGENERATION IN ZAMIA.

## CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY LXV.

JOHN M. COULTER and M. A. CHRYSLER.

(WITH EIGHT FIGURES)

MR. P. H. ROLFS, in charge of the Subtropical Laboratory of the United States Department of Agriculture at Miami, Florida, first called our attention to the remarkable power exhibited by mutilated stems of *Zamia floridana* of producing new shoots and roots. This cycad grows in great abundance in the neighborhood of the station, and ROLFS stated that he had seen "portions (of the stem) not larger than an English walnut" produce both shoot and root. He was kind enough to send an abundant supply of this mutilated and sprouting material, collected about February 1, 1904. The plants grow at Miami in a pure and well-drained sand, with a soil temperature standing rather uniformly at about 30° C. On April 16 ROLFS reported that the temperature of the soil one inch below the surface was 40° C.; three inches below, 38° C.; and six inches below, 35° C.

In most of the cases studied, the top of the thick stem had been cut off by the grubbing hoe, leaving the subterranean portion intact, though all of the smaller roots were lacking. Some of these stems were planted and observed at intervals. One of them, a plant about two years old, was placed in the greenhouse about February 13; the fully spread leaves soon withered, and no activity was visible for two and a half months, at the end of which time a new leaf was put forth from the bud. On June 1 the plant was removed carefully from the soil, its appearance being shown in *fig. 2*. The stem had been cut off at *x*, and had produced a new apex. Since the last planting no ordinary roots had been produced, though an upwardly directed spur 2 ᵐᵐ long (not shown in the photograph) indicated the beginning of one of the characteristic apogeotropic roots; and yet the young shoot was in vigorous condition.

An attempt was made to discover experimentally the possible

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anatomical limitations of this reproductive power, by artificial mutila-
tions of various kinds, but probably the proper conditions for vigorous
growth were not maintained; at least no results were obtained.

We have found no record of this behavior of Zamia, except in a
statement made by WILLDENOW,[1] a century ago, of which the follow-
ing is a translation:

> The majority of palms die as soon as their trunk is cut or even damaged.
> There are only a very small number of them which, like *Chamaerops humilis* and
> *Rhapis flabelliformis*, send out from their root new shoots; and *Cycas circinalis*
> is the only one which sends out shoots from its trunk when this has been cut;
> further, the stem of this tree gives out new roots where it finds itself in contact
> with the soil. The different species of Zamia may be cut up and thus multiplied
> artificially by cuttings, but with the exception of Cycas and Zamia no other palm
> survives amputation of the stem.

This power of producing new shoots and roots after mutilation
is usually called "regeneration," but this term seems to have been
applied primarily rather to the restoration of lost parts than to the
production of a complete new structure. As a consequence of its
broader application, there has been a tendency to regard the regenera-
tion ordinarily observed in plants and in animals as of two distinct
kinds; the former being nothing more than adventitious budding,
the latter actual restoration of lost parts, the new structure becoming
an integral part of the old. The great majority of the illustrations
of regeneration in plants are cases of adventitious budding rather
than regeneration in the stricter sense. We recognize the fact that
the whole subject of regeneration among plants is in an inchoate
condition, but perhaps the two kinds cannot be distinguished by any
exact definition. Most of the cases presented in this paper are not
regeneration in the restricted sense defined above, but in addition to
adventitious sprouting in Zamia there also seem to be cases of direct
restoration of lost parts.

In the mutilated (mostly decapitated) stems of Zamia studied,
the new shoots arise most frequently from the vascular part of the
central cylinder, as many as five shoots having been observed to
spring from this region in a stem 3 $^{cm}$ in diameter, though only one
shoot may occur. The vascular elements present in these shoots

[1]WILLDENOW, C. L., De quelques nouveaux palmiers de l'Amérique méridionale.
Mém. Acad. Roy. Berlin, 1804, p. 29.

are continuous with the vascular tissue of the central cylinder of the parent stem.

Less frequently, the new shoots arise from the peripheral part of the wounded surface of the cortex. Both of these regions of origin may be used in the same stem, as illustrated by *fig. 1.* In the case just referred to, a distinct group of vascular strands was traced from each shoot to the vascular tissues of the central cylinder.

In certain other cases no vascular connection was found, due probably to the fact that the shoots were younger and undifferentiated.

In a few cases the new structure stands directly over the central cylinder, as illustrated by *fig. 2* and observed also in much older plants. In such cases, a series of vertical sections shows that the vascular tissues of the central cylinder converge to form a dome-shaped cap underneath the restored part (*fig. 3*), that is, the whole cut end of the central cylinder regenerates, in the strict sense, the lost part being thus restored. In all other cases there is no such restoration, but the production of entirely distinct and complete structures upon the old stem. Just what conditions deter-



FIG. 1.—Decapitated stem showing one shoot growing from the vascular ring and one from the margin of the wounded surface.× ⅜.



FIG. 2.—Young plant which was decapitated at *x* and has produced a new apex. × ⅞.

mine the formation of a complete new structure in the one case, and the restoration of the lost part of the old structure in another case may not be clear, but it is entirely probable that the central cylinder is more apt to be restored in young plants.

The origin of the new roots is just as variable. It is customary to think of secondary roots as arising from vascular tissue, and this was found to be true in several of the cases studied. In the case illustrated by *fig. 4*, however, no trace of central cylinder was found, the piece of stem from which the shoot springs on one side and the root on the opposite side being simply a chip from the cortex of an old stem. Between this shoot and root of cortical origin a distinct and complete vascular connection was traced, the vascular elements forming a hollow cylinder tapering at the ends
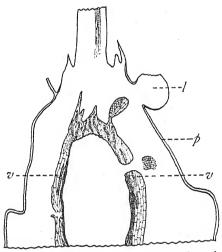


FIG. 3.—Median vertical section through apex of stem represented in *fig. 2: l*, base of leaf; *p*, periderm; *v*, vascular cylinder. × 4.

(*fig. 5*). It seems certain that the decay of the "chip" in this case would uncover a completely organized new plant. In any event, from this isolated cortex new organs and new kinds of tissue have been formed, the new shoot arising from the outer edge of the cortex in the region of the cork cambium, and the root arising from a more internal region of cortex. Whether the starting of the shoot determined the root, or *vice versa*, or neither, are matters of conjecture, but a completely organized and independent new plant has been derived from isolated and relatively old cortical tissue.

The attempt was made to determine the exact layer or tissue from which the new shoots proceed. It seems evident that regions of meristematic tissue alone are concerned, that is tissue which has either remained so or has resumed its power of cell-division; and in the ordinary cycadean stem there are at least three such active regions

in addition to the growing point, namely the fascicular cambium, the pericycle, and the cork cambium.   SIMON[2] finds that in regenerating root-tips the pericycle is the active layer.   In Zamia the pericycle is poorly differentiated, and does not act as a secondary cambium, as is the case in Cycas and certain other cycadean genera. In the cases observed the new shoots nearly always arise from the wounded surface; and as a layer of wound-phellogen is always found beneath this surface it must be added to the list of active regions.   It has been impossible thus far to secure the earliest stages in this adventitious shoot-formation, but sections through moderately young regions of this kind show the layer of callus curving outward around the base of the shoot-primordium (*fig. 7*).   This suggests that the phellogen forming the callus is responsible for the initial growth of the new shoot.   If this be true, a new shoot may be produced at any point of the surface covered by the callus.   In fact, in the cases of Zamia before us the new shoots stand over either fascicular cambium or cork cambium, but this position seems to us to be favorable rather than essential to shoot-formation.



FIG. 4.—A chip from the cortex that has produced a new shoot and root. × ⅔.

A case of the production of adventitious shoots from the hypocotyl

[2]SIMON, S., Untersuchungen über die Regeneration der Wurzelspitze. Jahrb. Wiss. Bot. **40**:103–143. 1904.

of a seedling was also observed (*fig. 6*). The photograph shows a leaf arising from a bud on one side of the hypocotyl; another bud, younger than the one shown, is present on the opposite side. Anatomical examination showed that the bud contains a strong vascular strand that runs straight inwards to join one of the bundles of the hypocotyl. A layer of periderm is present just beneath the surface of the hypocotyl, and around the bud this layer bends outward to form a sort of collar (*fig. 7*). The tissues of the bud show no evidence of breaking through the cortex, as is the case with lateral roots; hence it is probable that growth of the shoot started in the phellogen.



FIG. 5.—Vertical section through the piece shown in *fig. 4: l*, base of leaf; *p*, periderm; *r*, root; *v*, vascular cylinder. × 2.

Whether the bend of the hypocotyl indicates some slight injury or not cannot be answered, at least there is no direct evidence of an injury of any kind.

That a so-called polarity does not determine in this case the nature of the structure produced at each end of the mutilated stem, seems to be indicated by such a case as that represented by *fig. 8*, in which two new shoots and a root are arising from one end and a shoot



FIG. 6.—Seedling showing production of shoot from the hypocotyl. × ¾.

from the other.   It is probable that the horizontal position of the old stem is directly related to this result; and if so it would be referred to the influence of gravity.
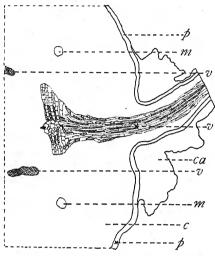


FIG. 7.—Part of transverse section through hypocotyl at level of the new shoot: *c*, cortex; *ca*, callus; *m*, mucilage duct; *p*, periderm; *v*, vascular strands.   × 10.

The suggested conclusions are that in the case of the stem of Zamia the power of regeneration and of developing adventitious shoots and roots is present in all meristematic tissue; that in cases of mutilation the meristematic tissue chiefly concerned is the phellogen of the callus, that over the region of the central cylinder being more often successful than that over the cortex.   This power does not seem to be localized in any definite points, such as have been called "latent buds," and which in this sense can have only a hypothetical existence; but is generally present in all meristem and expresses itself under favorable conditions.   The evidence against wounding as a necessary condition for such production of new shoots is suggestive, and that against the theories of "polarity" and "latent buds" seems to be clear.



FIG. 8.—Piece of stem showing two shoots and a root springing from one end and a shoot

# BRIEFER ARTICLES.

## NEW OR UNREPORTED PLANTS FROM SOUTHERN CALIFORNIA.

SPARGANIUM GREENEI Morong, Bull. Torr. Bot. Club **15**:77. *pl. 79, fig. 3.*—Collected near Ballona, in marshes near the coast of Los Angeles co., July 1904, by *Geo. B. Grant.* The type was collected at Olema, Marin co., and the plant is common there and at Lake Merced, near San Francisco, but has not been met with heretofore elsewhere.

POA HANSENI Scribner, U. S. Dept. Agric., Div. Agrost., Bull. **15**: p. 53. *pl. 9.*—In an alkaline meadow at Rabbit Springs, 2700$^{ft}$ alt., Mojave Desert, 4888 *Parish*, June 1901. This and the following grasses were identified at the Division of Agrostology of the U. S. Department of Agriculture.

POA LONGILIGUA Scribner and Merritt, U. S. Dept. Agric., Div. Agrost., Circ. **9**:3.—In open pine forests, Mill Creek Falls, 5500$^{ft}$ alt., San Bernardino Mts., 5043 *Parish*, June 1901.

POA SECUNDA Presl, Rel. Haenk. **1**:271.—Collected at the same time and place as the preceding species, and distributed under no. 5044.

ERAGROSTIS REPTANS Nees, Agrost. Parag. 514. *E. hypecoides* B. S. P. Prelim. Cat. N. Y. 69.—Los Angeles, *Rev. J. C. Nevin*, 1904. Probably a recent immigrant.

FESTUCA CALIFORNICA Vasey, Contrib. U. S. Nat. Herb. **1**:277.—Forest clad slopes, Mill Creek Mts., Head of Edgar Cañon, 4000$^{ft}$ alt., May 1881, 857 *Parish;* Mill Creek Falls, 5000$^{ft}$ alt., July 1892, 2490 *Parish.* The type of this species was collected near San Francisco, whence it extends to Oregon. The present report brings it nearly to the southern boundary of the state.

SITANION RIGIDUM J. G. Smith, U. S. Dept. Agric., Div. Agrost., Bull. 18:13.—Collected by *Mrs. H. E. Wilder*, June 1904, growing in the crevices of rocks on the summit of Grayback Mt., 11,725$^{ft}$ alt. The nearest station reported for this grass is Mt. Shasta, at the northern end of the state, but it may be expected on the intervening high summits of the Sierra Nevada.

JUNCUS TENUIS CONGESTUS Engelm. Trans. St. Louis Acad. **7**:450, Prairie Flat, 5,000$^{ft}$ alt., 3959 *Parish*, June 1895.

CHENOPODIUM LEPTOPHYLLUM Nutt., Moq. in DC. Prodr. **13²**:71.—I have a specimen of this plant collected long ago at Lang, Los Angeles co., by *Rev. J. C. Nevin*. Subsequent collectors appear to h ave overlooked it.

SAXIFRAGA PUNCTATA Linn. Sp. Pl. 401.—Dry Lake, Grayback Mt., about 9000$^{ft}$ alt., June 1904, *Mrs. H. E. Wilder*. Mt. Whitney, where it was collected by Coville, is the nearest recorded station, so that the present one becomes the southern limit of this species in the Sierra Nevada.

SPIRAEA DOUGLASII Hook. Fl. Bor.-Am. **1**:172.—Near the electric power-house in the cañon of the Santa Ana River, San Bernardino Mts. Collected in 1903 by *Miss Marguerite Graham*. The southern limit of the species.

**Horkelia Wilderae,** n. sp.—The whole plant sparsely pubescent: stems several from a perpendicular root, 2$^{dm}$ tall, slender, erect, much branched above: stipules lanceolate, entire or 1- or 2-toothed at base; basal leaves 6–8$^{cm}$ long; leaflets 5 or 6 pairs, cuneate, 5$^{mm}$ long, deeply incised, the few lobes oblong; upper cauline leaves unifoliate, deeply dissected: cyme diffuse: flowers numerous on slender pedicels, 3–8$^{mm}$ long: hypanthium glabrate, saucer-shaped, about 2$^{mm}$ in diameter; bracts linear-oblong, obtuse or acutish, 1$^{mm}$ long: calyx lobes lanceolate, 2$^{mm}$ long: petals obovate, white, about equaling the sepals: stamens 10: achenes 2 or 3.—Along the trail leading from Barton Flat to South Fork of Santa Ana River, 6000–8000$^{ft}$ alt., San Bernardino Mts., June 1904, *Mrs. H. E. Wilder*. The stems, and still more the calyces, are tinged reddish-purple, so that the whole plant appears of that color. Even the leaves soon become highly colored. Near *H. Michneri* Rydb., from which species it is well distinguished by its more diffuse cyme, smaller pedicellate flowers, and glabrous calyx lobes.

**Drymocallis viscida,** n. sp.—Viscidly villous throughout, with intermingled straight one-celled and crisped glandular several-celled hairs, which are sparse on the stems and abundant on the peduncles: stems several, erect, tinged with purple, about 3$^{dm}$ tall: stipules semiovate and acuminate-pointed, more or less toothed; basal leaves tufted, about 1$^{dm}$ long; petioles as long as the rachis of the pinnae, of which there are 3 pairs, 5–15$^{cm}$ long, orbicular to obovate, the terminal one cuneate, sessile; the lowest cauline leaves similar, the upper ternate to unifoliate, all coarsely incised-toothed: cymes rather condensed, few-flowered: bractlets narrowly lanceolate, 2$^{mm}$ long: sepals ovate-lanceolate, callous-tipped, 5$^{mm}$ long: petals yellow, obovate, a little shorter than the sepals, both merely spreading in anthesis; stamens about 20; filaments 1 to 1.5$^{mm}$ in the same flower.—

Snow Cañon, 5000^ft alt., San Bernardino Mts., 5060 *Parish*, June 20, 1901. Near *D. reflexa* Rydb., from which it differs in its smaller size, pubescence, and spreading sepals and petals.

TRIFOLIUM MONANTHUM TENERUM.  *T. monanthum* Eastw. Bull. Torr. Bot. Club **29**:81.—In meadows, at high altitudes in the San Bernardino Mts., Bluff Lake, 7400^ft alt., 3309 *Parish*, June 1894; Vivian Cañon, 6343 *Geo. B. Grant*, July 1904.

HOSACKIA TORREYI Gray, Proc. Amer. Acad. **8**:625.—Little Bear Valley, 5500^ft alt., San Bernardino Mts., *Mrs. H. E. Wilder*, September 1904.

PELARGONIUM AUSTRALE CLANDESTINUM Hook. Fl. N. Zea. 37.  *P. clandestinum* L' Her. ex DC. Prodr. **1**:660, as synonym.—Santa Ana, Orange co., *Rev. J. C. Nevin*, 1904.  Perhaps only adventive, or casual, but of interest as the second species of this genus collected in North America. The previously reported species is also from California, having been collected near San Francisco by Miss Eastwood. Identified by Dr. GREENMAN.

RHUS GLABRA Linn. Sp. Pl. 265.—Chino Cañon, near Palm Springs, at the desert base of San Jacinto Mt., November 1903, *H. E. Hasse*.  Dr. Hasse's interesting find adds the first true sumac to the state flora, the previously known species belonging to other sections of the genus.  This station becomes the western limit of the species.

**Gentiana viridula,** n. sp.—Annual: stem leafy, erect, simple, or few branched, 3–6^cm tall: leaves narrowly scarious-margined, the lowest orbicular, apiculate, 5^mm in diameter; the upper narrowly oblong, 5^mm long, obtuse, connate-sheathing: flowers solitary, terminal: corolla funnelform, 5^mm long; the lobes greenish, acute; the plaits at the sinuses blue, one-toothed: anthers oblong; filaments 1^mm long: capsule (immature) obovate, on a stout stipe 3^mm long.—Growing at the edge of water at the head of the South Fork of the Santa Ana River, 8500^ft alt., San Bernardino Mts., *Mrs. H. E. Wilder*, June 1904. §CHONDROPHYLLA Bunge, and near *G. prostrata* Haenke.

MENTHA CITRATA Ehrh. Beitr. **7**:150.—Well established along Town Creek, near San Bernardino, September 1904.  In the *Manual of the Bay Region*, Greene reports this mint from West Berkeley.  Apparently it is rather rare in the older states.

**Aster defoliatus,** n. sp.—About 1^m tall, minutely hispid above: stem leaves unknown, early deciduous; those of the pedicels narrow and bract-like, pungent, 3–8^cm long: heads in a loose elongated raceme, solitary or rarely 2 or 3 at the ends of the elongated leafy pedicels, small, 8^cm high and somewhat broader; bracts narrow, the green tips not much enlarged, loosely imbricated in a few series: rays about 40, light violet: achenes

hispid.—In a meadow at San Bernardino, 5335 *Parish*, October 17, 1903. This species belongs to Gray's subsection DIVERGENTES, and is quite distinct from any other Aster of Southern California.

ANTENNARIA MARGINATA Greene, Pitt. **3**:290.—Grayback Mt., about 7000$^{ft}$ alt., June 1904, *Mrs. H. E. Wilder*. A New Mexican species. Identified by DR. GREENE.

PSILOCARPUS TENELLUS Nutt. Trans. Am. Phil. Soc. **7**:340.—In the coastal subregion, probably not uncommon. San Diego, *Brandegee;* Glendale, near Los Angeles, *Braunton.*

**Senecio sparsilobatus**, n. sp.—A cespitose perennial, tomentose through-out: stems few, slender, 10–15$^{cm}$ tall: basal leaves 5–7$^{cm}$ long, the long petioles bearing near the end about five cuneate toothed pinnae 3–5$^{cm}$ long; those of the stem similar, but few and reduced: heads 1$^{cm}$ high, calyculate with 2 or 3 short filiform bracts, these glabrate on the margins; rays 8, disk flowers numerous.—Collected June 1904 by *Mrs. H. E. Wilder*, at about 7000$^{ft}$ alt., on the trail from Barton Flats to South Fork of Santa Ana River, in the San Bernardino Mts.

CENTAUREA CYANUS Linn. Sp. Pl. 911.—Well established at the race track, Los Angeles, where it was collected in the present year by the *Rev. J. C. Nevin.*—S. B. PARISH, *San Bernardino, California.*

# CURRENT LITERATURE.

## BOOK REVIEWS.

### The phenomena of fertilization.

FECUNDATION in plants is the subject of a treatise by MOTTIER[1] published by the Carnegie Institution, in which is discussed a variety of cytological topics. In judging the work the reader should bear in mind that the preface is dated August 1902, more than two years previous to the time of actual publication, a delay on the part of the Carnegie Institution that seems somewhat unjust to the author, and unfortunate in that it has withheld from investigators for many months an important contribution in a field of very active research where points of view change rapidly by reason of new discoveries. The book is chiefly a discussion of the nuclear activities connected with "fecundation," as the author prefers to call the fusion of sexual cells instead of using the more usual term fertilization.

Preliminary to the main discussion MOTTIER gives a general account of nuclear and cell division, based chiefly on his own work upon Dictyota and various types of the Liliaceae. There is a brief account of the centrosome and blepharoplast, the author believing that the latter structure arises *de novo* and holds no genetic relation to the former, which is the opinion of STRASBURGER, WEBBER, and others. The topic "significance of the sexual process and the numerical reduction of the chromosomes" is an excellent summary of STRASBURGER'S views on antithetic alternation of generations.

The last two-thirds of the work treats of sexual processes as understood in the plant kingdom, beginning with Ulothrix and Hydrodictyon and continuing through higher groups, without any attempt, however, at an evolutionary discussion. Indeed, the arrangement of forms follows closely the old classification of Sachs into zygosporic, oosporic, and carposporic types of sexual reproduction. Thus the arrangement of types of the Conjugales side by side with Sporodinia under the heading "non-motile isogametes" seems a very artificial division, in view of the many recent studies on multinucleate gametes (coenogametes). It is among the thallophytes that the work is likely to suffer most from the advancing investigations, and since 1902 papers on the coenogametes of several ascomycetes have appeared, also accounts of oogenesis in Vaucheria and Saprolegnia, while the recent work of WOLFE on Nemalion is likely to change very materially our conception of the morphology of the sexual organs in the Rhodophyceae.

The account of the archegoniates and angiosperms describes in detail the

[1] MOTTIER, D. M., Fecundation in plants. imp. 8vo. pp. viii+187. *figs. 75.* Washington, D. C.: Published by the Carnegie Institution. 1904.

structure of the sperms of the pteridophytes and the sexual processes in Onoclea, Cycas, Zamia, Ginkgo, Pinus, and for the angiosperms Helleborus and Lilium. Among these higher forms every month is bringing forth important papers and there are no cytological topics in which the ground has so frequently shifted and is still so unstable as that treating the events and significance of synapsis and heterotypic mitosis and the behavior of chromosomes during reduction and fertilization.

The work deserves special mention for its clear exposition of the chief theories of STRASBURGER on subjects associated with sexual reproduction. It is the most complete account of the speculations of this master published in English and should be very welcome to the general reader.

The book is very fully illustrated and the figures excellent, but they would have been even clearer if printed on a paper with a smoother surface.—B. M. DAVIS.

GUÉRIN[2] has brought together in a very useful way for French readers our information in reference to fertilization and associated phenomena in seed-plants. Spermatogenesis, oogenesis, and fertilization in angiosperms are first presented; and the same topics are taken up under gymnosperms, the Cycadales, Coniferales, and Gnetales being considered separately. In each case a brief historical résumé is given, and the references to recent bibliography are fairly complete, surprisingly so in the case of American publications. There are numerous illustrations, and the orderly presentation of topics makes the work very easy to consult. Of special interest in a work issued from GUIGNARD's laboratory is the full presentation of "double fertilization." Brief concluding chapters deal with a comparison of angiosperms and gymnosperms as to the origin and development of the reproductive structures and the phenomena of fertilization, a comparison of the phenomena of fertilization in plants and animals, and a general interpretation of the phenomena of fertilization. The work is a compact organization of current knowledge, and should be of great service in calling the attention of French botanists to the more modern points of view in connection with seed-plants.—J. M. C.

### Botany among the ancient Greeks.

WHILE ALL botanists have heard of THEOPHRASTUS, and know that he wrote a treatise on plants, it is safe to assume that only a few have taken the time to read him in the original. We have had translations of his Ἱστορίαι τῶν φυτῶν, but now for the first time there is before us a critical study of this work, as well as the works of other Greek and Roman writers.[3] It appears that the stimulus for the Ἱστορίαι was largely given by the reports brought back from India by those who accompanied Alexander the Great upon his journey of conquest.

[2] GUÉRIN, PAUL, Les connaissances actuelles sur la fécondation chez les Phanérogames. pp. vii+160. Paris: A. Joanin et Cie. 1904. 10 *fr.*

[3] BRETZL, HUGO, Botanische Forschungen des Alexanderzuges. 8vo. pp. xii+412. *figs. 11. maps 4.* Leipzig: B. G. Teubner. 1903. *M* 12.

The original reports of the officers of this expedition are lost to the world, perhaps forever, but THEOPHRASTUS had access to them, and has presented their observations on plants, together with his own.  BRETZL, the author of the work, believes that THEOPHRASTUS deserves to rank among the great botanists of the world, and that he was the only great botanist of antiquity, so far as we have record. PLINY, in comparison, is regarded as an inaccurate copyist.  It is certainly remarkable that at the very earliest dawn of botanical study so many correct observations should be made, observations, too, which have commonly been lost sight of even until now.  Nearly all of the important observations made by THEOPHRASTUS have been reported as original by modern botanists.

A few of the more striking contributions made by the Greeks may be here mentioned.  Mangrove swamps were reported about the Persian Gulf, and this record is the only one we have of them; they have not yet been "originally" reported by modern botanists; SCHIMPER says that, with the exception of Avicennia, mangroves have not been seen west of the Indus.  The descriptions of the mangroves are so exact that one has no trouble in making out the character species as we now know them.  The zonal relations of the species were noted, Rhizophora being correctly regarded as the pioneer.  It was inexplicable to them, as it is to us still, that plants, and particularly trees, could grow in salt water. Similar geographic studies were made in the deserts of Beluchistan, and there, as in the mangrove swamps, the character plants were described as such.  THEOPHRASTUS used a series of leaf types in his descriptions, based largely on ecological features; more than two thousand years later, HUMBOLDT made out a similar series, and largely because of this has been generally regarded as the father of plant geography.  The nyctitropic movements of the tamarind leaf are carefully described and are definitely termed sleep movements, distinction being made between leaves of that type and those of Mimosa.  The banyan is correctly regarded as a fig, and the supporting roots are called roots and not stems, because they are leafless, and not green; their adventitious character is also noted.  Compound leaves are so regarded in spite of the leaf-like appearance of the leaflets; the reasons given are the fall of the entire structure in autumn, and the fact that in the buds the leaflets are not differentiated.  The sexuality of plants is clearly shown, especially in cucurbits and dates, and use is made of the terms male and female.  Nearly two thousand years later, CAMERARIUS again showed the sexuality of plants, although it was late in the century just past before it was universally accepted.—HENRY C. COWLES.

## Biological statistics.

DAVENPORT'S *Statistical methods*[4] has been revised and enlarged and made to embody all the more important recent developments in the mathematical analysis of variation in living organisms, as elaborated chiefly by PEARSON and

[4] DAVENPORT, C. B., Statistical methods with special reference to biological variation. 2d. ed. 16mo. pp. viii+223. *figs. 10.* 1904.  New York:  John Wiley & Sons. For review of first edition see BOT. GAZ. **28**: 364. 1899.

his students. Much of the book has been rewritten and many additions of new examples and new methods are given, making it more indispensable than ever as a handbook for the student of this important phase of biology.

The changes which have been made are too numerous to be considered in detail, but the most noticeable are as follows. (*a*) The section is omitted which dealt with the quantitatve expression of terms used by botanical taxonomists in the description of leaf-form. (*b*) The subject of correlation has received new and altogether better treatment by the substitution of YULES's method for DUNCKER's, and the addition of PEARSON's method for determining the correlation between qualities not quantitatively measurable. (*c*) Two additional types of asymmetrical curves are presented. (*d*) A section is introduced dealing with MENDEL's law of alternative inheritance. (*e*) A 22-page chapter on the results of statistical biological study is substituted for the 2-page chapter on the applications of statistical methods. (*f*) A professedly complete bibliography is given instead of a selected one.

A comparison of the bibliography with that given in the first edition shows in an interesting way the remarkable activity which has developed in this field. In the earlier edition thirty-nine titles were given, in the present edition there are 265 references, 186 of which bear dates later than the date of publication of the first edition. As is usual in extensive bibliographies the attempt at completeness leaves something to be desired. A number of titles not found in the list occur to the reviewer as being of more value statistically than some which are given.

The unique feature of the chapter on the results of statistical studies is a tabulated analysis of the literature, showing the general bearing, and in some instances the point of view, of each paper. At least two of these papers are listed under subjects to which they make no significant contribution; *e. g.*, HARSHBERGER on "The limits of variation in plants" and KELLERMAN on "Variation in *Syndesmon thalictroides*" are classed as dealing with correlation, but neither paper treats specifically of questions of correlation, and the data given by each are too meager to be of value to students who would be interested in turning them to account in the study of correlations.

Everyone will appreciate how difficult it must be to keep free from errors a work made up so largely of tabulations. A reference on p. 113 to Table X means Table X of the first edition, which has become Table XII of the present edition. Botanists will be astonished to see *Syndesmon thalictroides* classed as a desmid on p. 78.

On the whole, the second edition is a very marked advance over the first, and there is every reason to expect that with its assistance the bibliography of statistical biology will rapidly advance in the coming years, not alone in the number of titles but also in the clearness and completeness of mathematical analysis and in the importance of the conclusions reached.—GEORGE H. SHULL.

### Gasteromycetes of Hungary.

Hollós's[5] imposing monograph of the Gasteromycetes of Hungary, the German edition of which has recently come from the press, will form one of the most valuable additions to the literature of this group. One cannot read the introductory parts of this work without feeling that the most careful and critical attention has been given to every detail.

In 1896 the author, as he tells us, began to devote exclusively to the study of the gasteromycetes the time that his duties as teacher in the Staatsoberrealschule in Kecskemét left at his disposal. From this time until the completion of the work material was collected principally by innumerable excursions into the various parts of Hungary, while many specimens were received from collectors throughout the country. By purchase or exchange the author was able to secure numerous types from other European countries and from America, thus making possible a direct comparison of specimens representing species common to these countries. The scope of the study was still further widened by visits to all the important collections of gasteromycetes in Europe.

In the work, which is a large folio volume, eighty-one species and many varieties are described and illustrated. These represent all the forms known to occur in Hungary. To the technical descriptions the author has added his own observations, both adding to the original description and pointing out many peculiarities of appearance or form occurring during the different stages of the growth of the plants. These incidental characters, that are too often omitted in descriptions, bring to the mind a clearer picture of the plant in question than the categorical enumeration of technical characters. The text includes complete citations of specimens seen by the author, enabling the future student to identify the plants which the author had in mind or his descriptions and drawings. A full list of synonyms is found at the end of the descriptive portion.

The work contains thirty-one beautifully executed plates, printed by a color-type process from colored drawings and from colored photograph. In the illustrations the author has endeavored to represent specimens showing the different stages and forms in which the fungus is likely to be found. Variable species are more fully illustrated. Five plates are devoted to the forms of *Secotium agaricoides*. Microscopical details are added in most cases.

The complete descriptions, full synonymy and citation, and the excellent illustrations are three features that will insure this book a position of authority among taxonomic works. Not only will it be of value to the students of the country for which it was written, but also to American students, for most of the gasteromycetes have a world-wide distribution. Of the forms described nearly all occur in this country and specimens of many of these were seen and cited by the author. —H. Hasselbring.

## Two recent books on algae.

A VERY readable text on British fresh-water algae by G. S. WEST[6] has appeared
and will be welcomed as the only work of its kind in English that is up to date.
The descriptive portions of the book are clear and the figures excellent.   The
accounts of the desmids, diatoms, and unicellular green algae deserve special
mention.   The general arrangement of the groups is quite simple and consistent
from the author's point of view, but few specialists would be likely to agree with
him, so varied are the classifications of the algae.   WEST'S arrangement is in the
main conservative, and the synopses and keys are so clear that the reader cannot
be confused.   There is a preliminary account of methods of reproduction, sexual
organs, polymorphism, and phylogeny.   These topics might well have been
expanded, as in their condensed form a reader with little knowledge of mor-
phology is scarcely likely to grasp the underlying homologies and evolutionary
principles illustrated in the algae.

Much more pretentious is a large volume of OLTMANNS[7] which is announced
as the special part and is to be followed shortly by a second that will treat of general
problems.   OLTMANNS covers the entire group of the algae, fresh water and
marine, excepting the Cyanophyceae, and aims to collect all important literature
of recent years.   His classification is elaborate, and the arrangement of the great
groups is quite different from that in *Die natürlichen Pflanzenfamilien.*   How-
ever, the families are easily understood, and it is around them that the descriptive
matter is collected in convenient form.   Reproductive processes are discussed in
great detail, especially for the Phaeophyceae and Rhodophyceae, where the
advance in our knowledge has been greatest in recent years.   The account of the
Rhodophyceae, following his interpretation of the cystocarp as involving a sporo-
phytic generation associated with the gametophyte, is an especially valuable con-
tribution, bringing order into what has been one of the most chaotic subjects in
botany.   The work is very full of figures, some 470, excellently reproduced, many
of them covering the greater part of the page.   This first volume is sure to find a
hearty reception and the second one will be awaited with keen interest.—B. M.
DAVIS.

## Index Bryologicus.

THE *Index Bryologicus* of Général PARIS[8] was completed in 1894 and a sup-
plement was published in 1900.   It was welcome as a real boon to bryologists
and the immense toil of its author was gratefully appreciated.   Now it has been

[6] WEST, G. S., A treatise on the British freshwater algae. 8vo. pp. 372. *figs.
166.* Cambridge University Press. 1904. 10s. 6d.

[7] OLTMANNS, F., Morphologie und Biologie der Algen. Vol. I. 8vo. pp. 733.
*figs. 467.* Jena: Gustav Fischer. 1904. *M* 20.

[8] PARIS, E. G., Index Bryologicus sive enumeratio muscorum ad diem ultimam
anni 1900 cognitorum, adjunctis synonymia distributioneque geographica locupletis-
simis. fasc. II. 8vo. pp. 65–128. Paris: Librairie Scientifique A. Hermann. 1903
2.50 *fr.*

determined to recast the work and to supply certain deficiencies, especially in dates of publication and in Scandinavian literature, bringing the work down to the beginning of the twentieth century as a point of departure for future investigations.

The original was unfortunate in usually omitting the dates of publication of species; the prospectus announces that in the second edition this lack will be supplied. Yet the second fascicle (which alone has just reached us) shows many failures to carry out this laudable intention. *Nomina nuda* (admitted in the first edition in hope of proper publication!) will be rigorously excluded, it is said, but the *Index* will include besides described species and those issued in numbered exsiccati, species "existant dans les grands herbiers publiques (Kew, British Museum, Paris, etc.) où on peut les consulter." The latter have no place in such a work and should be as rigorously excluded as other *nomina nuda*.

The author of so important a bibliographical work should have adopted a consistent system of citation and adhered to it rigidly. Much space might have been saved and greater clearness attained by attention to such details. References "*loc. et op. cit.*" are maddening because they compel the users to hunt back for the last citation often some lines back and not prominent enough to catch the eye readily. Even with its faults the revision of this indispensable *Index* will be greatly appreciated. We trust the publisher will take due pains to make its dress accurate and worthy of this valuable work. It is to be issued in monthly fascicles of which about 25 will be needed.—C. R. B.

### Wiesner and his school.

THE PERSONALITY of a great investigator is very properly recognized upon festal days by his associates and pupils. Hofrat Professor Dr. WIESNER founded in 1873 the institute for plant physiology in University of Vienna, and upon the occasion of the thirtieth anniversary of his professorship his many pupils have united in congratulations, and a *Festschrift* [9] has been prepared by three of them, which takes the form of a contribution to the history of botany. After a congratulatory introduction by Dr. HANS MOLISCH it consists of two parts. In the first is a bibliography of WIESNER'S writings, which number 213 titles extending over fifty years (1854-1903), and a running summary of his contributions to various subjects, classified so as to facilitate ready reference. As a second part there is a bibliography of 157 titles and a similar résumé of the work by his pupils which has issued from this institute. The first part was prepared by Dr. LUDWIG LINSBAUER of the Imperial Gymnasium and Dr. KARL LINSBAUER of the Institute (Professor Wiesner's assistant), and the second by Count LEOPOLD VON PORTHEIM, of the Biologische Versuchsanstalt recently established in the Prater.

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[9] LINSBAUER, K., LINSBAUER, L., and PORTHEIM, LEOPOLD R. VON, Wiesner und seine Schule; ein Beitrag zur Geschichte der Botanik. Festschrift anlässlich des dreissigjährigen Bestandes des pflanzenphysiologischen Institutes der Wiener Universität. Mit einem Vorwort von Prof. Dr. HANS MOLISCH. 8vo. pp. xviii+260. Wien: Alfred Hölder. 1903.

Among the names in the second bibliography one finds those of BURGER-STEIN, CZAPEK, FRITSCH, HABERLANDT, KRASSER, LINSBAUER, MIKOSCH, MOLISCH, WETTSTEIN, ZAHLBRUCKNER, and others—certainly a notable list. It has been a pleasure to many American botanists to meet Professor WIESNER this summer and to join in the congratulations upon his past labors and extend to him our best wishes for the future.—C. R. B.

## MINOR NOTICES.

FRITSCH has published an interesting contribution to the comparative morphology of the seedling of Gesneriaceae.[10] The account is so largely a description of many forms that a satisfactory summary is difficult to give. The book is divided into two parts. In the first part twenty-six species, comprising fourteen genera, are treated, and the gross form, particularly in several species of the Streptocarpus, is described in considerable detail. In the second part the structure of the grown plants is considered, and the behavior of the cotyledons, leaf arrangement, anisophylly, and kindred topics presented by this group are discussed. A chapter is devoted to a short account of the anatomy of Gesneriaceae and one also to the structure of Steptocarpus as compared with other Cyrtandroideae.—W. B. MacCallum.

THE HORTICULTURAL SOCIETY of New York has published[11] the proceedings of the International Conference on plant-breeding and hybridization held in New York city, September 30 and October 1 and 2, 1902. The conference was such a notable one in the quality of the papers presented that it is a valuable service to biology in general to have them accessible. Not only are the presented papers published, but also the discussions and the papers read by title. Forty-two papers are thus brought together, most of them dealing with the fundamental principles of plant-breeding and hydridization, and they represent investigations and conclusions that botanists should become more familiar with.—J. M. C.

LINDAU[12] has published a pocket handbook for the collection and preparation of the lower cryptogams with special reference to conditions in the tropics. In this work of some 75 pages the characteristic habitats of mosses, liverworts, algae, and fungi are described; directions are given for the preparation of material in herbarium form and for the simpler methods of preserving in spirits or in formalin. It is a book which the traveler and collector with botanical interests will find very useful.—B. M. DAVIS.

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[10] FRITSCH, K., Die Keimpflanzen des Gesneriaceen, mit besonderer Berücksichtigung von Streptocarpus, nebst vergleichenden Studien über die Morphologie dieser Familie. 8vo. pp. iv+188. *figs. 38.* Jena: Gustav Fischer. 1904. $M$4.50.

[11] Proceedings International Conference on plant breeding and hybridization. 1902. Hort. Soc. N. Y. Memoirs, Vol. I. New York: Horticultural Society. 1904.

[12] LINDAU, G., Hilfsbuch für das Sammeln und Präparieren der niederen Kryptogamen mit besonderer Berücksichtigung der Verhältnisse in den Tropen. 12mo. pp. 78. Berlin: Gebrüder Borntraeger. 1904. $M$1.50.

THE TWENTIETH part of ENGLER's *Das Pflanzenreich* is a presentation of the great tropical family Zingiberaceae by SCHUMANN.[13]    The usual critical discussion of the family from various standpoints is followed by a presentation of the 38 genera and 849 species.  Four new genera (*Odontychium*, *Gagnepainia*, *Aframomum*, *Monocostus*) and 141 new species are described.—J. M. C.

ROTH's *Europäischen Laubmoose*[14] progresses rapidly, the eighth part having been issued in July and the ninth in October.  They contain the conclusion of the Acrocarpae and a good share of the Pleurocarpae.  It would seem that two more parts might complete the work.  The author would do well to devote a final part to keys to genera and species.—C. R. B.

THE SECOND fascicle of the third volume of HALÁCSY's[15] flora of Greece completes the work, including from Gramineae through the pteridophytes.  With this last fascicle appear the general preface, the bibliography, an introduction describing the floristic regions, and a good index.—J. M. C.

## NOTES FOR STUDENTS.

BESSEY[16] has described the peculiar stomata of *Holacantha Emoryi*, a leafless shrub of the southwestern arid regions.  The guard cells lie at the bottom of a narrow chimney-shaped cavity which extends above and below the epidermis, and consists of about eight vertical rows of cells.—J. M. C.

THE MORPHOLOGY and general histology of three Pacific coast algae are described in the last number of the Minnesota Botanical Studies:[17] *Callymenia phyllophora* by CLARA K. LEAVITT; *Endocladia muricata* by FLORENCE M. WARNER; and *Laminaria bullata* by OLGA MUELLER.—B. M. DAVIS.

RUSSELL[18] shows many photographic prints produced by contact or mere approximation of various woods with a sensitized plate in darkness.  The amount of action varies greatly with different woods, exposures of thirty minutes to eighteen hours or more being required.  The active agent seems to be $H_2O_2$, and probably the resin in the wood is the indirect cause.—C. R. B.

[13] ENGLER, A., Das Pflanzenreich. Heft 20. Zingiberaceae von K. SCHUMANN. pp. 458.  Leipzig: Wilhelm Engelmann. 1904.  *M* 23.

[14] ROTH, GEORG, Die europäischen Laubmoose. Leiferung 8, pp. 257–384. *pls. 21–30.* Leiferung 9, pp. 385–512. *pls. 31–40.* Leipzig:  Wilhelm Engelmann. 1904.  Each *M* 4.  Not sold separately.

[15] HALÁCSY, E. de, Conspectus Florae Graecae.  Vol. III. fasc. 2. pp. 321–520. Leipzig: Wilhelm Engelmann. 1904.  *M* 6.

[16] BESSEY, CHARLES E., The chimney-shaped stomata of *Holacantha Emoryi*. Bull. Torr. Bot. Club **31**:523–527.  *pl. 24.* 1904.

[17] Minnesota Botanical Studies **3**:291–308. *pls. 44–47.* 1904.

[18] RUSSELL, W. J., On the action of wood on a photographic plate in the dark. Phil. Trans. Roy. Soc. London B. **197**:281–289. *pls. 11–18.* 1904.

SCHULZE[19] has investigated quantitatively the formation of arginin in various stages of the germination of *Lupinus luteus*. He finds it is produced entirely from proteid decomposition, probably through the action of erepsin, a protease. The facts adduced seem to support his contention that asparagin is a secondary product, because it is not formed *pari passu* with decomposition of proteids as arginin is.—C. R. B.

MOLISCH reports[20] an extraordinarily rapid autonomous movement of the leaves in *Oxalis hedysaroides* HBK., far exceeding the oft-described movements of *Desmodium gyrans*. In the latter the leaf completes its elliptical path in 85–90 seconds at a temperature of 35° C., while in the former the tips of the leaflets may sink at once 30–45°, or a distance of 5–15$^{mm}$, in a single second, though the movement may consume twelve seconds and be executed in a succession of six jerks, with a pause of about a second between. The recovery occupies about five minutes.—C. R. B.

THE RESULTS of SCHOUTE[21] on the histogenetic layers of *Hippuris vulgaris* have been called in question by KNIEP[22] who considers that SCHOUTE studied too few specimens and used unsuitable methods. From a renewed study of the growing point in a large number of stems of Hippuris, KNIEP concludes that the histogenetic layers of HANSTEIN correspond to the regions distinguished by VAN TIEGHEM, thus going back to the old accepted view. It is unfortunate for this theory that Hippuris is the only flowering plant in which the histogenetic layers of the stem are distinguishable.—M. A. CHRYSLER.

SCHIFFNER calls COKER sharply to account[23] for overlooking his characterization of Dumortiera as having rudimentary air-chambers and so misrepresenting him.[24] He contends that the obliteration of the air-chambers is not an adaptation to a moist habitat, as COKER suggested, nor dependent on exposure to light, as STEPHANI held. Observations in Java and the constancy of *D. trichocephala* and *D. velutina* under cultivation for twenty years in the Vienna botanic garden are adduced in favor of his view that the extent of development of the air-chambers is a fixed and heritable character of each species.—C. R. B.

THE JOINTED structure peculiar to some genera of the corallines in the red algae has been studied by YENDO.[25] These regions of the plant are free from

[19] SCHULZE, E., Ueber die Argininbildung in den Keimpflanzen von *Lupinus luteus*. Ber. Deutsch. Bot. Gesells. **22**:381–384. 1904.

[20] MOLISCH, HANS, Ueber eine auffallend rasche autonome Blattbewegung bei *Oxalis hedysaroides* HBK. Ber. Deutsch. Bot. Gesells. **22**:372–376. *figs. 2.* 1904.

[21] See review in BOT. GAZ. **35**:144. 1903.

[22] KNIEP, H. Sur le point végétatif de la tige de l'*Hippuris vulgaris*. Ann. Sci. Nat. Bot. VIII. **19**:293–303. 1904.

[23] SCHIFFNER, V., Ueber Dumortiera. Hedwigia **43**:428. 1904.

[24] COKER, W. C., Dumortiera. BOT. GAZETTE **36**:225. 1903.

[25] YENDO, K., A study of the genicula of Corallinae. Jour. Coll. Sci. Imp. Univ. Tokyo **19**:—. [pp. 41. *pls. 1.*] 1904.

the lime which is deposited between the cells in all of the nodes. The form of the genicula are frequently of important taxonomic value and they present several types of structure, the pitted structure being described and figured. The pits are both lateral and terminal and consist of depressions which extend to the middle lamella where there is a lens-shaped thickening which, however, lies in the middle of the cavity and does not completely close the pit.—B. M. DAVIS.

MISS FORD[26] has published a somewhat detailed account of the anatomy of Psilotum. The plant is monostelic throughout, being protostelic at the base of the aerial stem and often siphonostelic above. In the aerial branches a central core of sclerenchymatous fibers is found, and throughout the phloem is poorly developed. The form is probably a reduced one, but the anatomical evidence does not relate it closely to any of the living Lycopodiales. There is closer resemblance to certain Lepidodendron forms; but the combination of sporangial and anatomical characters is closest to Sphenophyllales, as BOWER has suggested.— J. M. C.

THE DEVELOPMENT of sieve tissue in conifers has been studied by CHAUVEAUD,[27] who describes elements intermediate between sieve tubes and parenchyma occurring in the hypocotyledonary portions of *Abies Pinsapo*, though not found in the higher regions of the stem. These elements are succeeded by the primary phloem, and both are eventually squeezed to a flat mass by growth of the secondary phloem. In another paper[28] the same author shows that the double leaf trace in the genera Abies and Pinus is single in the leaf of the seedling, and in the course of ontogeny splits into two, that is the double leaf trace is a secondary formation.—M. A. CHRYSLER.

DENNISTON[29] finds in developing starch grains of various sorts an outer sharply defined layer of material next the plastid which takes up orange strongly from the safranin gentian-violet orange stain, while the body of the grain becomes bright violet. Grains partly digested by diastase show the orange-staining layer little affected, while the violet regions are much dissolved and orange-staining material appears in the corroded interior. DENNISTON interprets these reactions to mean that the outer layer is different from the rest (MEYER was able only in a few cases to find such a layer in potato starch) and, in harmony with TIMBERLAKE's study of the developing cell wall, believes it to be a carbohydrate not yet fully polymerized to starch.—C. R. B.

[26] FORD, SIBILLE O., The anatomy of *Psilotum triquetrum*. Ann. Botany 18: 589–605. *pl. 39.* 1904.

[27] CHAUVEAUD, G. Le liber précurseur dans le sapin pinsapo. Ann. Sci. Nat. Bot. VIII. 19:321–333. 1904.

[28] CHAUVEAUD, G. Origine secondaire du double faisceau foliare chez les sapins (Abies) et les pins (Pinus). *l. c.* 335–348.

[29] DENNISTON, R. H., The structure of the starch grain. Trans. Wis. Acad. 14: 527–533. 1904.

FROM A series of experiments in which the radicles of seedlings were employed as physiological reagents, DANDENO[30] concludes that the theory of electrolytic dissociation is without support from the physiological side. The author also finds, as TRÜE and OGLEVEE have already shown,[31] that the toxic effect of certain solutions is greatly reduced by the mere presence of non-chemical bodies, such as pure sand whose property of physical affinity retards chemical action and physiological effect. The economic significance of these facts is also stated. Other factors regarded as affecting toxicity of solution are quantity of solution, rate of diffusion, shape of container, and even the glass walls of the container. —RAYMOND H. POND.

TWO NOTES of interest in relation to the way in which the powdery mildew and downy mildew live through the winter are published by ISTVÁNFFI.[32] As is well known the perithecia of the powdery mildew rarely occur in Europe, and according to the author they have not been found in Hungary. Patches of mycelium, however, are said to remain alive during the winter on the stems and dried clusters of grapes left on the vines. From these fresh conidia were produced when taken into the laboratory in January. Similar observations, the author states were made by APPEL. The mycelium of the downy mildew is also found[33] to survive the winter in parts of the vine, especially in the buds, thus confirming the observations of CULONI.—H. HASSELBRING.

To ASCERTAIN the influence of a periodical dry season upon the meristematic activity of the cambium, URSPRUNG[34] has studied the anatomy of certain species common to Buitenzorg and East Java. The climate of the former locality is uniform, while that of the latter shows a distinct periodicity of wet and dry seasons. He finds as a general rule (for representatives of six different families) that material from East Java shows a much more complete and distinct zonation of wood structure than specimens of the same species from Buitenzorg. Species vary, however, in susceptibility to climate, since the one which shows the relatively clearest zonation in Buitenzorg may not sustain this relation in a group of the same species from East Java. The influence of foliation and defoliation upon

[30] DANDENO, J. B., The relation of mass action and physical affinity to toxicity, with incidental discussion as to how far electrolytic dissociation may be involved. Amer. Jour. Sci. IV. **17**:437–358. 1904.

[31] TRUE, R. H., and OGLEVEE, C. S., The effect of the presence of insoluble substances on the toxic action of poisons. Science N. S. **19**:421. 1904.

[32] ISTVÁNFFI, GY. DE, Sur l'hivernage de l'oïdium de la vigne. Compt. Rend. Acad. Sci. Paris **138**:596–597. 1904.

[33] ISTVÁNFFI, GY. DE, Sur la perpétuation du mildiou de la vigne. Compt. Rend. Acad. Sci. Paris **138**:643–644 1904.

[34] URSPRUNG, A., Zur Periodicität des Dickenwachsthums in den Tropen. Bot. Zeitung **62**[1]:189–210. 1904.

the activity of the cambium is given some attention, but no general conclusion is established.—RAYMOND H. POND

SEVERAL METHODS in cytological technique are described by OSTERHOUT.[35] One of these is a substitute for the universally used paraffin method. Though various soaps have been tried and found unsatisfactory, OSTERHOUT has developed a method with cocoanut oil soap which he regards as superior to the paraffin method. It is better to make one's own soap, using 70$^{cc}$ of cocoanut oil to 38.5$^{cc}$ of 28 per cent. solution of caustic soda in water. The tissue is placed in warm water and the soap added gradually until a fairly strong solution is obtained. It may then stand in the bath for two or three days. When sufficiently firm, the block may be cut. The sections form a perfect ribbon and do not crumble or crush as is so often the case with paraffin. They may be fixed to the slide with albumen. In trying this method one should have the full paper at hand.— CHARLES J. CHAMBERLAIN.

THE GREAT and, indeed, almost violent interest taken in some quarters in Bulletin 22 of the U. S. Bureau of Soils, will cause the appearance of Bulletin 23 to arouse some curiosity at least.[36] The subject-matter of the present bulletin falls into two separate portions. The first presents a series of rather incomplete experiments on the movement of soil water, together with some data on the rate of imbibition of seeds in contact with moist soil, while the second portion deals with experiments on the growth of plants in culture media. The first mass of material is not important, but the second presents a discovery which, if substantiated and generally true, is as far-reaching and important as it is unexpected. This discovery is, briefly, that the good or bad characteristics of a soil are transmitted to its aqueous extract. This is shown by growing wheat plants in pots of the soils to be compared and in bottles of watery extract of these same soils. In such an experiment the different water cultures show the same relations as do the pot cultures. The plants were compared in respect to size and general appearance and to amount of transpiration. That this difference in soils and their solutions is not one of mineral salts is shown by the fact that good and poor Cecil clay show the difference markedly, although practically identical in chemical nature. It is suggested that the bad properties of at least some sterile soils may be due to organic substances. The bulletin is essentially a report of progress and all of its lines of investigation will need further work before they can be regarded as established.—B. E. LIVINGSTON.

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[35] OSTERHOUT, W. J. V., Contributions to cytological technique. (1) A simple freezing microtome. (2) Fixation *in vacuo*. (3) A simple slide holder. (4) A rapid method of mounting in aqueous media. (5) Embedding microscopic algae. (6) Embedding with incomplete dehydration. Univ. of California Publications. Botany 2:73-90. 1904.

[36] WHITNEY, M. and CAMERON, F. K., Investigations in soil fertility. U. S. Dept. Agric., Bureau of Soils, Bull. 23. 1904.

MISS MATTHAEI[37] has made a careful study of the effect of temperature on photosynthesis, which by avoiding radical sources of error corrects the resul s of various observers and particularly those of KREUSSLER, which have been accepted and quoted for more than a decade. Having found that the actual temperature of a leaf was not that of the water bath within which it was placed when high intensity of light was used, thermoelectric measurements of temperature became necessary. A thermocouple of copper and constantan wires only $.087^{mm}$ in diameter was imbedded in the midrib of the leaf used and was connected with a galvanometer to which also a second thermoelement in a water bath was connected. When this bath was brought to such a temperature that there was no deflection of the needle the temperature of the element in the leaf was known. The results show that corresponding to each temperature there is a definite maximal amount of photosynthesis which cannot be reached unless both light and $CO_2$ supply are adequate. These maxima increase with increasing temperature, forming a curve convex to the temperature abscissas which resembles the respiration-temperature curve. They begin to decrease suddenly some degrees below the temperature which can be endured only a few hours. The maximum photosynthesis at any temperature can be maintained only for a short time, declining the sooner the higher the temperature. The difficulties overcome in the experimentation and the manipulative skill exhibited make this a notable contribution to plant physiology.—C. R. B.

KUYPER[38] has given an account of the events of the development of the ascocarp of *Monascus purpureus* Went and *M. Barkeri* Dangeard. The account of the former agrees in the main with that recently given by IKENO,[39] but differs in some respects. The sequence of events is as follows: The ascogonium consists of two cells, the lower of which develops. No fusion was observed between the ascogonium and pollinodium. The number of nuclei in the ascogonium increases. "Free cells" are then formed possessing one to several nuclei. The 1-nucleate stage is regarded as having arisen from the fusion of the nuclei of the originally binucleate cell, a view opposed to that of IKENO, who believes the cells to appear with single nuclei. In the next stages the number of nuclei in each free cell increases to a considerable extent. It appears that the spores are now formed within the free cells. These are represented as containing a variable number of nuclei, one to many, so that the whole spore is deeply stained. According to IKENO each spore contains but a single nucleus while the other nuclei of the free cell degenerate. When mature the spores fall apart and come to lie free in the

[37] MATTHAEI, GABRIELLE L. C., Experimental researches on vegetable assimilation and respiration. III. On the effect of temperature on carbon-dioxide assimilation. Phil. Trans. Roy. Soc. London B. **197**:47–105. *figs. 6.* 1904.

[38] KUYPER, H. P., De perithecium-ontwikkelung van *Monascus purpureus* Went en *M. Barkeri* Dangeard in verband neet de phylogenie der Ascomyceten. Dissertation. pp. 148. Amsterdam. 1904.

[39] IKENO, Ueber Sporenbildung etc. Ber. Deutsch. Bot. Gesells. **21**:259. 1903.

ascogonium.  The account of *M. Barkeri* follows the same general outline with some differences as to details.  The protoplasm of the ascogonium is divided into sections by irregular vacuoles.  These sections become free cells within which the spores are formed.  In the summary one spore is said to be formed from each of the eight nuclei in the free cell; in the text, however, the spores are described as possessing many nuclei.  The paper contains also a long discussion of the Hemiasci and the phylogeny of the ascomycetes.—H. Hasselbring.

NATHANSOHN[40] continues his investigations of the nature and functions of the plasmatic membrane in plants.  The following points are now announced.  If slices of Dahlia tubers be placed in 2 per cent. $Na_2S_2O_3$ solution for two days, they absorb the salt to such an extent that at the end of the experiment its concentration within the tissues is about one-sixth of that without.  If now these slices be changed to a solution of the same salt of a concentration equal to that now within the tissue, there occurs a marked outward diffusion, so that at the end of another two days the inner concentration is considerably less than one-half of the outer one.  This means, of course, that the salt has passed through the plasmatic membrane in a direction from the weaker to the stronger solution, *i. e.*, against its own diffusion tension.  This case substantiates similar results already published by the same author.

Furthermore, slices of the tubers of *Helianthus tuberosus* and of the roots of the red beet placed in solutions of $NH_4Cl$, $NH_4NO_3$, $(NH_4)_2S_2O_3$, $(NH_4)_2SO_4$, and $(NH_4)_2HPO_4$, absorb much more of the ammonium ion than of the anion.  This is not accompanied by an increasingly acid reaction of the external solution.  The last observation led to an investigation of the substances which might diffuse out from the cells, and enough Mg was found to have escaped to account for about three-fourths of the $NH_4$ which had entered.  The author supposes that some other cations, perhaps in part organic bases, must be given out from the cells, and thus explains the lack of acidity.  It is possible also to cause the extrusion of Mg by subjecting these tissues to a solution of a potassium salt.  K is absorbed and Mg replaces it in the external solution.

A very interesting theoretical discussion makes up a good part of the paper, in which the nature of the protoplasmic layers is considered in the light of the new facts, but this cannot be entered into here.—B. E. Livingston.

BRIGGS and McCALL[41] have devised an ingenious method for investigating soil solutions and the rate of movement of such solutions in the soil.  The apparatus consists, briefly, of a porous porcelain filter tube connected with a vacuum chamber.  The wall of the tube is saturated with water, and in this condition it can be exhausted to the vapor pressure of water, and will maintain this nearly

[40] NATHANSOHN, A., Weitere Mitteilungen über die Regulation der Stoffaufnahme. Jahrb. Wiss. Bot. **40**:403–442. 1904.

[41] BRIGGS, L. J. and McCALL, A. G., An artificial root for inducing capillary movement of soil moisture.  Science N. S. **20**:566–568. 1904.

complete vacuum against atmospheric pressure for a day or more. The tube thus prepared and connected to a two-liter vacuum chamber is placed in the soil to be studied. The water surfaces of the pores in the tube become continuous with the surfaces of water films in the soil, and water moves into the tube at a rate which varies with the nature of the soil and its amount of contained moisture. The force involved in the movement of water through the wall of the tube is the difference between the capillary pressure or surface tension of the water surfaces at the external and internal ends of the pores of the wall. And since the external surfaces are continuous with those of the soil water, it follows that water must pass from the soil into the tube, for the soil films are subjected to a pressure of one atmosphere, while those at the internal surface of the tube bear a pressure only equal to the vapor pressure of water. The authors do not make this matter immediately clear, and it may simplify matters to call attention to the fact[42] that the films of tube and soil form a system one extremity of which (in contact with the vacuum) is subjected to a very low pressure, while the other extremity (in contact with the air) is subjected to a pressure relatively very great. Thus in the end the solution is driven through the tube by atmospheric pressure, though the steps in the movement involve the forces of capillary films.

The rate at which water collects in the tube is the criterion for the soil's power of delivery. The authors state that the nature of the collected solution is the same as that of the soil itself, though proof of this is reserved for a later paper.—B. E. LIVINGSTON.

ERIKSSON[43] has published two further accounts bearing on the mycoplasma theory of rust fungi. These accounts deal with *Puccinia dispersa* Eriks. on rye and *P. glumarum* Eriks. & Henn. on barley. The facts, according to the author, are these. The teleutospores of *P. glumarum* are capable of germinating immediately after ripening in midsummer. Aecidia occur on *Anchusa arvensis* and *A. officinalis*. During thirteen years' observations the aecidia were observed only in three instances in the vicinity of Stockholm. Both because the aecidium is produced from the teleutospores in summer or autumn, and on account of its rare occurrence in this region, it cannot be the source of spring infections of rye. It is also impossible to find living mycelium in the plants during the winter. These facts point to the conclusion that the infection arises from a germ already existing in the seed. In the leaves sectioned during the winter the author found peculiar dense protoplasm which he considers as a mixture of the protoplasm of the host and of the fungus mycoplasm. Later the nucleus is partially dissolved, while "nucleoli" begin to appear in the mycoplasm. This stage occurs immediately

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[42] This method of statement has been hinted at in a review of this article by KING. Either this reviewer has failed to grasp entirely the meaning of the authors or his own statements are so ambiguous as not to warrant a discussion of his criticisms here. See KING, F. H., An artificial root for inducing capillary movement of soil moisture. Science N. S. **20**:680–681. 1904.

[43] ERIKSSON, J., Ueber das vegetative Leben der Getreiderostpilze. Kungl. Svensk. Vet.-Akad. Handl. **38**:—. [no. 3. pp. 18.] *pls. 3.* 1904.

before the appearance of uredosori. In the next stage intercellular protomy-celium begins to appear. The patches of mycelium are connected with the "nucleoli" mentioned above. These are the centers of development for the inter-cellular mycelium. The course of development of *P. glumarum* follows the same lines.

Some of the author's figures admit of a different interpretation from that given. It is difficult to see how a nucleus being dissolved by a substance diffused throughout the cell as the mycoplasm would be can be cut away on one side in such an abrupt way as figured in *pl. 1*. It would seem possible that the proto-plasmic connections extending from nucleoli to the intercellular protoplasm represent haustoria, for, to use the author's own words, they give exactly the same impression as a young haustorium of the Uredineae.—H. HASSELBRING.

THE REGULATION of turgor in molds is again the subject of study, this time by PANTANELLI,[44] working with Aspergillus. The author points out that, since in these organisms the cell walls are normally in a state of tension owing to the pressure within, the method of plasmolysis is not available directly as a measure of turgor pressure. Incipient plasmolysis will occur only after the application of an external pressure which is equal to the normal pressure of the vacuole plus that of the stretched wall. He further shows that the pressure which influences the wall is made up of at least three components: the osmotic pressure of the vacuole, the pressure of swelling of the protoplasm itself (*Quellungskraft*, closely related, if not identical with the pressure of imbibition in organic bodies), and the tension of the surface films. The latter is exerted toward the center of the cell, and is negligible when compared with the other two which are exerted in the opposite direction. An ingenious method for approximating these two outwardly directed forces is used in the work. It is based on measurement of cell shrinkage in plas-molyzing solutions. To control the results obtained by plasmolysis, the method of determining the freezing-point of expressed sap is resorted to.

Cells of this form live but a few days and practically all the cells of a culture die when spores are produced. Thus it is necessary to be sure one works with at least a great majority of living cells. The pressure of swelling decreases with age of the cell, while the osmotic pressure of the sap first rises and later falls, but is always dependent upon the pressure of the nutrient medium. The total turgor pressure of a cell depends in great measure upon conditions of nutrition, rising with increase of sugar in the medium, sinking with lack of oxygen. Other con-ditions, such as temperature changes, anaesthetics, etc., affect turgor pressure, and the author is convinced that in these changes we have a true response within the protoplasm itself. When the fungus responds to sudden increase in external osmotic pressure, its adjustment takes place at a rate which is related to the velocity of penetration into the protoplasm of the solute used. This leads to the idea that the perception of the osmotic stimulus occurs only when this solute has distributed itself throughout the protoplasm.—B. E. LIVINGSTON.

44 PANTANELLI, E., Zur Kenntnis der Turgorregulationen bei Schimmelpilzen. Jahrb. Wiss. Bot. **40**:303–367. 1904.

# NEWS.

Professor W. Pfeffer has been elected a corresponding member of the Vienna Academy of Sciences.

F. M. Rolfs has been appointed professor of botany and horticulture in the University of Florida, at Lake City.

R. S. Williams, who has been collecting in the Philippines for the New York Botanical Gardens, has lost his collections of four months by fire in a hotel where he was making his headquarters.

Professor N. L. Britton, director of the New York Botanical Garden, received the honorary degree of D.Sc. from Columbia University in connection with the recent celebration of the one hundred and fiftieth anniversary of its foundation as King's College.

Bernard Renault, the well-known paleobotanist at the Museum of Natural History in Paris, died October 16, 1904, at the age of sixty-eight years. His studies of the conspicuous vegetation of the Coal Measures have been of the greatest possible service to anatomists and morphologists.

Professor W. A. Kellerman, of the Ohio State University, will spend the first three months of the coming year in Guatemala. He expects to traverse the country from east to west, and to spend considerable time in the Andes Mountains. The purpose of the trip is to collect parasitic fungi, and incidentally to execute some small botanical commissions.

The former students of Professor Charles E. Bessey who are connected with the Office of Vegetable Pathology and Physiology, Department of Agriculture, have had an enlarged copy of his photograph framed and presented to the office. The portrait was unveiled by Dr. E. A. Bessey, at a gathering of the office staff on November 28. Miss Carrie Harrison presented the picture, and appropriate remarks were made by Messrs. Woods, Webber, and Shear.

# GENERAL INDEX.

The most important classified entries will be found under Contributors, Personals, and Reviews. New names and names of new genera, species, and varieties are printed in **bold-face** type; synonyms in *italics.*